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The relation between cell, nuclear and chromosome dimensions in a sterile violet species-hybrid[1]

W. P. Pierce

(WITH PLATE 4 AND THREE TEXT-FIGURES)

In general it may be said that the data from the numerous investigations of chromosome numbers and sizes, in relation to hybridization potentialities and to the incidence of sterility and fertility, are conflicting. An analysis of older views which dealt with the problem of development from the point of view of cell interactions, i.e., rate and plane of cell division, is infrequent in current literature. The present writer feels that this method of approach perhaps might be a fruitful one. The study of Sinnott on *Acer* (1930) and of Sinnott and Kaiser (1934) on the morphological development of the fruits of *Cucumis* and *Cucurbita* are examples of this method of approach to the problem. The latter authors have secured highly interesting data on the growth rates at various stages of development, and have been able to correlate factors of cell growth with the emergence of fruit form.

In view of the comprehensive knowledge of chromosome number in the species of the genus *Viola* (Clausen, 1927, 1929, 1931; Gershoy, 1934) and the known relation of the number to species characters and potentiality of species hybridization, it seemed here advisable to attempt to relate chromosome number in the plants herein studied to the dimensions of the cells, nuclei, and chromosomes and to the amount of chromatin present in the nucleus. One purpose of the study was to determine the relation of such data to the problems of morphogenesis in species and species-hybrids.

In an effort to analyze the concept of the individuality of the chromosome, a portion of the study was devoted particularly to the careful measurement of somatic chromosomes in root tips. The direct bearing of this hypothesis upon the chromosome theory of heredity is obvious. Such supporting evidence as has been presented by Moenkhaus (1904), Baltzer (1909), and Tennent (1908), was concerned with the recognition of smaller and larger chromosomes in the hybrids. It would seem that in addition to such an approach, the theoretical importance of the problem requires a careful study of chromosome sizes in both parents and the hybrid. The apparent lack of a decisive difference in chromosome form in the genus *Viola*, between the small chromosomes making up a gametic

[1] Published with the approval of the Director of the Vermont Agricultural Experiment Station.

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set (haploid-genom), leaves, as an alternative approach to this problem of individuality, the study of chromosome size.

The following observations embody the results of a statistical study of the characteristic cell, nuclear, and particularly the chromosome size relationships of the root tips of two species of *Viola* bearing unlike chromosome numbers, and the sterile species-hybrid derived therefrom. Cell size was investigated, in part to correlate if possible comparative size differences with nuclear and chromosome dimensions, and in part to compare with cell sizes of the mature tissue of the stem and leaf.

HISTORICAL

The literature pertaining to the individuality of the chromosome has been presented comprehensively in texts as, for example, Wilson (1925), and Sharp (1926, 1934). In general while the evidence is conflicting it may be said that most of it supports the theory rather than opposes it. As Wilson has pointed out, much of the evidence is very indirect, such as for example the constancy of chromosome numbers from one cell generation

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Explanation of plate 4

Figures 1a, 3a, 5a, were drawn with the aid of a camera lucida, using a Zeiss 2 mm. apochromatic objective and a 20× compensating ocular. The projected magnification obtained was approximately 3100×. Each chromosome was numbered to facilitate counting and to permit accurate identification in measurement. Figures 1b, 2, 3b, 4, 5b, 6, represent photomicrographs taken with the aid of a Zeiss 2 mm. apochromatic objective and a 20× compensating ocular, on an Eastman process film, at approximately 1700×. The source of illumination was an improved Zeiss lamp, used with a prism reflector.

Fig. 1a. *V. papilionacea*, 2n = 54, inner periblem cell two cells outside of endodermis, from mature root tip.

Fig. 1b. *V. papilionacea*, 2n = 54, photomicrograph of cell drawn in figure 1a, at a smaller magnification.

Fig. 2. *V. papilionacea*, 2n = 54, photomicrograph of epidermal cell of mature root tip. Note that upper left corner of plate is out of focus.

Fig. 3a. *V. conspersa*, 2n = 20, inner periblem cell, one cell removed from the endodermis.

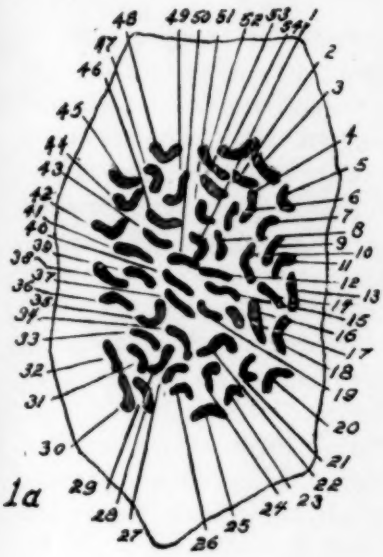
Fig. 3b. *V. conspersa*, 2n = 20, photomicrograph of cell drawn in figure 3a, at a smaller magnification.

Fig. 4. *V. conspersa*, 2n = 20, photomicrograph of cell located directly beneath the hypodermis.

Fig. 5a. *V. conspersa* × *papilionacea*, 2n = 37, epidermal cell of mature root tip.

Fig. 5b. *V. conspersa* × *papilionacea*, 2n = 37, photomicrograph of chromosomes drawn in figure 5a, at a smaller magnification.

Fig. 6. *V. conspersa* × *papilionacea*, 2n = 37, photomicrograph of epidermal cell of mature root tip.


1a

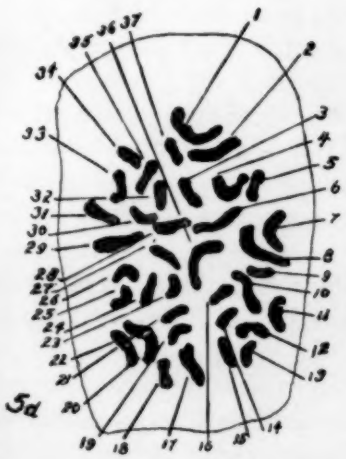
1b

2

3d

3b

4


5d

5b

6

to another. Some investigators, however, have shown more definite data not only in constancy of chromosome number but in size and shape as well. The amount of work done on different genera, in which the karyotypes of the numerous species have been studied, is enormous.

Direct evidence for the persistent individuality of chromosome form, however, has been recently presented by McClintock on *Zea* (1931). This investigator, by demonstrating the presence of "genetic markers," has been able to trace discrete portions of chromosomes in various types of translocations and inversions, and to correlate such changes in chromosome form with genetic data. Her studies are being currently extended in investigations on corn and other genera.

Earlier data have been presented to demonstrate that there seems to be a persistence of the definitive chromosomes even through the resting stage of the nucleus. Richards (1917), using as material the eggs of *Fundulus*, has shown that the condensed chromosomes of the metaphase become vesiculated and that the nucleus is virtually made up of a group of separate elementary nuclei, or karyomeres, the boundaries of which though contiguous do not merge. Boveri (1909) had earlier demonstrated a somewhat similar condition in *Ascaris*, in which the nuclear lobes (representing chromosomes) present in the telophase reticulum, tended to assume the same relative positions in the following prophase. Although these lobes were similar in shape and position, they were confluent in the center of the nucleus. Kater (1928) indicates from his work on species of three different genera of plants that the reconstruction of daughter nuclei in somatic root tip tissue is accomplished by essentially the same process. The genera used were *Solanum*, *Lycopersicon*, and *Allium*, with chromosomes ranging in size from very small in *Solanum* to large in *Allium*. Although the drawings he presents do not show a persistent organization as clearly as do those of Richards, he suggests that chromosome vesiculation is probably the universal method of nuclear reconstruction.

Interesting data in confirmation of the individuality of the chromosome is that described by Wenrich (1916) for the grasshopper *Phrynotettix magnus*. In this insect certain chromosomes are individually recognizable by persistent characteristics of size, form and position of chromomeres, and behavior. After a careful study of the individual chromosomes during spermatogenesis, he concluded that the chromosomes retain their individuality and that each one possesses a definite organization which is expressed in the relative sizes and position of its chromomeres. He shows figures of one pair of prophase chromosomes in thirteen different individuals, all of which appear to be comparable. Though the concept of the existence of chromomeres as discrete portions of the chromosome has

been recently criticized, the method of carefully studying the individual chromosomes appears to be the best method of approach to the problem.

The theory of individuality has been attacked by various investigators. As Wilson states, Fick (1907) and Della Valle (1909, 1912) were among the first, the viewpoint of the latter having been presented by Wenrich. Della Valle likened chromosome formation to the formation of liquid crystals, and maintained that their identity was wholly lost in the resting nucleus. Wilson replies to the criticism that the chromosomes are temporary and variable structures, by asserting that it is a weakness to consider the chromosomes en masse, without further regard to their individual characteristics.

On the other hand, Morita (1927) finds a variation in number as well as in the size of chromosomes in the first spermatocyte of the orthopteran *Necrostethus grossus* (Linn.) and he concludes that it is difficult to harmonize his findings with the theory of chromosomal individuality.

Chamberlain (1925) from his studies of cycads concludes that both cytoplasm and chromatin are vacuolated and of essentially the same structure. "Definite chromomeres upon a linin ribbon afford a convenient resting place for genes, and facilitates philosophical speculation, especially if a theory demands a rigid serial arrangement of hereditary characters in the spireme. In a vacuolized chromosome there might be some serial arrangement, but it could not be so definite." Finally "he predicts that theories which cannot be reconciled with a vacuolated structure of the chromosome will have to be abandoned."

Avdulov and Titova (1933) in a study of additional chromosomes in *Paspalum stoloniferum*, showed that the heteroploid (23) chromosome individual possesses all the chromosomes of the normal set (2n–20) plus three small ones. Analysis of the morphological characters of plants with 20 and 23 chromosomes showed no difference of the phenotype. Hence the authors conclude that in their case the additional chromosomes seem to exert no influence on the phenotype. Furthermore, in some cases species notably akin morphologically differ sharply in their karyotype. The two to four surplus chromosomes lead to no essential changes in the structure of the corresponding organism. These authors avoided the apparent contradiction with the theory of localization of hereditary factors in chromosomes by regarding the additional chromosomes as vestigial. Yet the data secured in the recent work on extra-chromosomal types in *Datura*, by Sinnott, Houghtaling and Blakeslee (1934), demonstrate the influence of additional chromosomes on chromosomal balance and in turn on the anatomy of the mutants. Thus, the complexity of the relationship between

the presence of the additional chromosomes (and their contained genes) and the effect on the organism, is indicated.

Delage and Goldsmith (1919) in a general critique of mendelism, acknowledge the great advances in the field of genetic research, but think that there are many defects and uncertainties, and above all a fragility of the objective bases upon which mendelism rests. Their reasons for questioning the continuity of the chromosomes are: (1) They are not visible in the resting stage (in a few genera this may be questioned). (2) The linear arrangement of the genes is questioned because chemical differentiation within the individual chromosomes has not been demonstrated. (3) They contend that a force which will bring homologous chromosomes into such an intimate and accurate alignment as is necessitated by the chiasmatypy hypothesis will not permit them to lie cross-wise and give cross-overs. (4) They maintain that the mendelian conception gives no explanation of the successive appearance of characters in ontogeny, or of the origin of new characters in evolution. Finally they predict the collapse of mendelian concepts because of the weight of accessory hypothesis needed to explain special cases.

The work of Mathews (1924) would indicate that from a bio-chemical point of view the evidence is at best negative as regards any support for chemical differentiation in chromatin.

MATERIAL AND METHODS

Fixations. The root tips used were collected from plants grown in the greenhouse under conditions as nearly identical as possible. It was found that the plants were thriftier and produced better tips if they were transplanted and then allowed to grow in well aerated soil for several weeks. Care was taken to remove the surrounding soil from the roots by means of a gentle stream of water. Only the youngest and most healthy tips were selected for fixation, and these were from mature plants.

Two different killing fluids were employed: 1. La Cour's (1931), which he assumed to be especially adapted to root tip fixation, yielded fairly satisfactory results. 2. A modified S. Navashin solution[2] seemed to be the more satisfactory method at least with violet root tip material. Sections were cut eight to ten microns thick and stained in Heidenhain's iron alum-haematoxylin, care being taken to insure as uniform treatment as possible on the various sets of root tips.

[2] Developed in the cytology laboratory at this Station the proportions of fluids being as follows: To 180 cc. of Webber's modification of Navashin's fluid, 60 cc. of Flemming's medium solution was added to part A.

Cell Measurements. The method used in measuring cell areas of the dermatogen of the root was almost exactly the same as was used by Marvin (1936) in measuring areas of the cells of the stem and leaf. In each case 200 cells were drawn by means of a camera lucida at a magnification of 1500 times and the magnified drawings were measured with the planimeter. Longitudinal cell lengths were measured directly by means of an ocular micrometer at the same magnification as were the nuclear diameters.

Chromosome Measurements. All the chromosomes measured were first drawn with a camera lucida from carefully selected metaphase plates, at a projected magnification of 3100 diameters, with the aid of a Zeiss 2 mm. apochromatic objective and 20× compensating ocular. Higher magnifications, such as have been used by Navashin (1931) on *Crepis*, and by Lorbeer (1930) on *Sphaerocarpus*, entailed in the present case a distinct loss in clarity and definition of the outline of the chromosomes.

The measurements of the drawings were taken by means of a small strip of fairly heavy, pliable paper, carefully ruled in millimeters. The length of the middle axis of the chromosome drawing could thus be measured by means of this strip, despite the occurrence of curvatures in a horizontal plane. This simplified method was found to be quite effective. Navashin used a somewhat similar method but one which differed in the respect that his measurements were taken by means of dividers with the points set 3 mm. apart. He judged that he had attained by his method an accuracy of two to eight percent of the individual chromosome length (depending upon its total length) and two to five percent of the total length of the whole chromosome set.

It is evident that a source of error in measuring chromosome lengths may be due to a foreshortening caused by the curvature of a chromosome away from the horizontal plane. Navashin has criticized the projection method of Kagawa (1929). The latter attempts to reconstruct the actual chromosome length by a determination of the vertical distance involved in an upward or a downward curvature. Yet Navashin has pointed out that the measurement of vertical distances by means of the micrometer screw can hardly exceed an accuracy of less than one micron. Inasmuch as most of the vertical curvatures observed in the chromosomes here studied extended upward or downward only a fraction of a micron, it was thought best to disregard such curvatures when present. It seems, moreover, that in measuring chromosomes with several such curvatures the probable error would be high.

In the case of the violet roots careful focusing on the selected plates of the material used clearly indicates that some chromosomes show a

foreshortening, but that most of the chromosomes measured extended in a horizontal plane on the equatorial plate. This fact could also be verified by examining longitudinal sections of tips, in which the chromosomes were seen on the spindle from the side. At full metaphase not only are they apparently quite separate from each other, but in general they tend to lie in one plane. Such errors as result from the method of measurement employed doubtless give figures which are less than the actual values for the chromosome length because, where foreshortening has occurred, it has been disregarded for the reasons stated above. As can be seen from the photomicrograph of the chromosomes of *V. conspersa* (plate 4) their greater average length might show more of an error of this sort than the shorter chromosomes of *V. papilionacea*. Stated otherwise the error would be greater in longer chromosomes than in shorter ones. However, as Navashin has pointed out, since only relative values are required, a slight undervaluation of the actual length is permissible throughout.

The magnified chromosome lengths, recorded in millimeters, were transposed to their actual values in microns.

OBSERVATIONS AND DATA

Chromosome size in relation to cell and nuclear volume in the meristem of the root

The measurement of comparable cells in the root was undertaken to determine whether there exists on the one hand a constant cell size characteristic in any given tissue, and a correlation between cell volume and chromatin mass on the other. In order to measure cell volume two sets of measurements were necessary, i.e., (1) cross section areas and (2) longitudinal lengths of cells in the given tissue. The weighted mean area multiplied by the weighted mean cell height is a measure of cell volume. Obviously these two sets of measurements cannot be taken from the same root but must come from root tips which are as nearly comparable in size as possible. Although open to criticism for this reason, no other method seemed practicable in determining the volume of such cells.

As a measure of chromatin volume, both the total chromosome length of the diploid complement and the volume of the nucleus were used. It is apparent that in an estimate of nuclear volume the nuclear sap, the chromatin, and the achromatic substance are all included. It is likely that of the two methods the measurement of the total chromosome lengths alone gives a more accurate estimate of the amount of chromatin present in the nucleus. Of the two sets of data the greatest range of variation, from cell to cell, seemed to occur in the measure of total chromosome lengths.

Navashin (1931), whose earlier work dealt with a study of cell volume in relation to chromatin mass, measured total chromosome lengths alone. He has used this measure of chromatin volume without consideration of chromosome width, although admitting that widths between pure species may vary greatly. Furthermore, Navashin in his later paper (1934) states (page 196) that "great as this difference may be it disappears always whenever the chromosomes which display it are brought together in a hybrid cell." In the case of the material dealt with here the width of the chromosomes of *V. papilionacea* was less than the width of those of *V. conspersa*, while in the hybrid cells these initial differences still seemed to be apparent in the hybrid genom. It seems obvious, therefore, that while a measure of total chromosome length may serve as an estimate of the amount of chromatin, the chromosome width should not be disregarded.

I. Cell Measurements

Cross section areas. Bruun (1932) has recently re-emphasized that environmental factors probably operate less in the modification of the root tip meristem than in that of the shoot. For this reason, as well as the more obvious one that differentiation processes are practically absent, he considers the root tip meristem ideal to show a specific cell size. In examining a cross section of a violet root tip it is immediately apparent that not only does cell size vary appreciably from one tissue to another, but that it exhibits a wide range within a single tissue. In general, the parenchyma cells of the plerome tend, in any one cross section, to be smaller than those of the cortex or of the epidermis. The periblem displays the greatest variation in cell size, which ranges from the small innermost cells to the large cells of the hypodermal layer, which are the largest cells of the promeristem. The epidermis, which is made up of a single cell layer, contains cells of a size which is somewhat less than that of the hypodermis. Because the epidermis is but a single layer thick, and also because it shows a fairly narrow range in size variation as compared with the periblem, it is a favorable region for study.

Young (1933) measured carefully the cell lengths and breadths of five tissues of the apical three millimeters of corn roots. His observations showed that the transitional characters of each tissue could be observed separately. Each tissue seemed to have characteristics peculiar to itself as regards region of greatest division, time and speed of elongation, etc. Young favored the earlier view of Haberlandt (1914) that the three histogens of the root may in certain cases be traced to the common initial zone at the apex of the root.

The observations of the present writer made upon violet root tips,

considered in the light of Young's literature review, would seem to favor either Haberlandt's view, or perhaps would fall into the second class proposed by de Bary (1877) in which the plerome is sharply defined, but the periblem and dermatogen are united at the apex of the root. The position of the cross sections used in the present work lay in the upper half of the first millimeter and extended into the second millimeter. The exact distance from the tip was not determined as accurately as were those of Young, but the region was fairly defined by the number of sections from

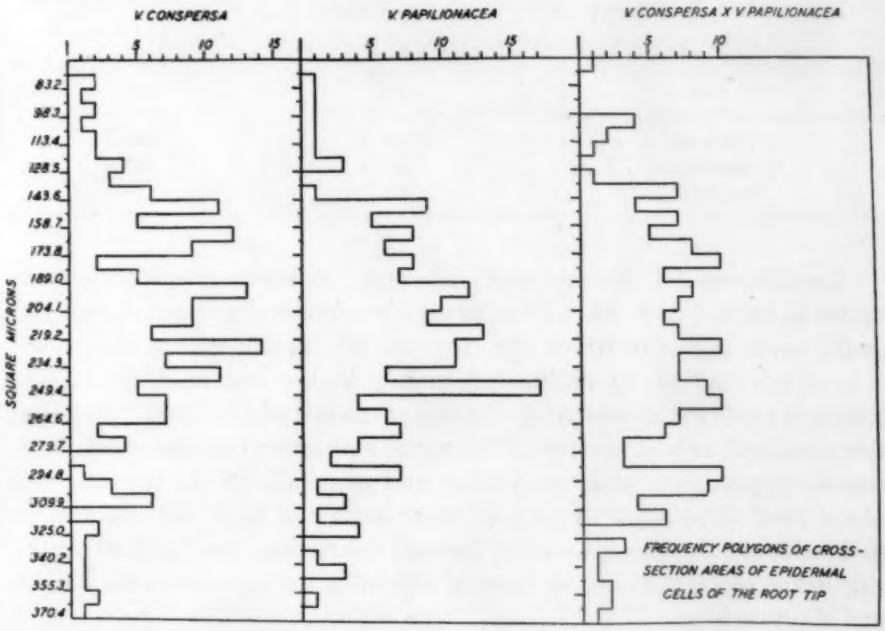


Fig. 1. Explanation in the text.

the tip. From similarly placed quadrants in serial cross sections, in an upward progression, strips including an average of ten adjacent cells were drawn in outline.

The data shown in the frequency polygons (fig. 1) are summarized in the following table (1). From the figures obtained it is apparent that there is present in the epidermis of the root of both species, a characteristic cell size. It also appears from the data that the mean cell size in the hybrid is intermediate.

From the figures presented in the table it may be observed that there exists a difference of approximately 12% between the mean cross section area of the epidermal cells of the parent species. Though the modal class shows figures of a somewhat higher value, there is almost an equivalent

difference, namely 10%. As can be seen from an examination of the graph, no definite modal class could be established in the measurements of the cells of the hybrid. However, the weighted mean cross section areas tabulated above seem to indicate that the area of the epidermal cells of the hybrid tends to be intermediate between the two parent species. It is to be noted further from the graph that the total range of cell areas, though rather wide in extent, seems to correspond very closely in the two species and the hybrid.

TABLE 1

Cross section areas of epidermal cells in square microns (see fig. 1)

PLANT	MEAN	MODE
V. conspersa	210.9	226.8
V. papilionacea	229.8	249.4
hybrid (C×P)	214.3	—

Longitudinal cell measurements. The measurements of epidermal cells shown in table 2 were taken from median longitudinal sections of root tips in the same region in which the cross section measurements were made (i.e., upper half of 1st millimeter, mainly in the 2nd millimeter). The length of a cell was measured on the axis of the cell parallel to the periclinal (longitudinal) axis of the root. The upper and lower transverse cell walls usually appear parallel to each other and perpendicular to the long axis of the root. Where one or both of these walls had been laid down at an oblique angle, the length on a line through the median, longitudinal central axis of the cell was recorded, thereby obtaining the average of the longest and shortest height.

Examination of table 2 showing the frequency distribution of cell lengths, indicates a rather wide range, varying from 6.6 to 22.8 microns. As less than one hundred measurements were taken from each parent and the hybrid, a well-defined modal class cannot be deduced from the table. A weighted mean, however, has been computed in each case from the measurements recorded, and is given at the bottom of the table. As in the case of the cross section areas there is again some evidence that in the hybrid there exists an intermediate expression, here shown in cell height.

It is of interest to note at this point a rather unusual method of cell elongation (stretching) which was apparent in a few tips cut in median longitudinal section. These particular roots indicate what seems to have been a periodicity in stretching of the cells of the epidermis, first along the radial and then along the vertical longitudinal axis of the cell. The expression of this periodicity or rhythm was such that four or five cells

would appear shortest along the radial or horizontal axis and at the same time longer along the vertical axis. Directly above this region, the cells would show an exactly reverse condition, the cells becoming wider and shorter. This gradual, alternate expansion along two different planes,

TABLE 2

Frequency distribution of the longitudinal measurements of the dermatogen cells of the root

MICRONS	PLANT		
	V. CONSPERSA	V. PAPILIONACEA	HYBRID C×P
6.6	1		
7.2	1		
7.8	1		1
8.4	8	1	3
9.0	4	2	1
9.6	18	0	2
10.2	2	1	6
10.8	9	5	7
11.4	0	0	4
12.0	12	4	13
12.6	1	1	3
13.2	2	4	4
13.8	3	1	3
14.4	2	5	4
15.0	2	4	6
15.6	4	3	5
16.2	1	1	1
16.8	2	7	1
17.4	0	2	1
18.0	2	9	3
18.6	0	3	1
19.2	1	4	1
19.8		2	0
20.4		5	2
21.0		3	0
21.6		1	1
22.2		0	
22.8		2	
Mean:	10.8	15.7	12.8

persisted back along the tip as far as the region of cell elongation. Freisner (1920) has shown a daily periodicity in cell division to occur in the root tip which may perhaps be reflected in the above configuration.

The observation made by Young (1933) that in the epidermis cell division was most active toward the upper half of the first millimeter rather than at the very apex, was observed to hold true in the present investigation.

II. Nuclear Measurements

TABLE 3

Nuclear measurements from cells of the epidermis showing frequency of distribution of diameters in microns

PLANT	FREQUENCY									
MICRONS	6.6	7.2	7.8	8.4	9.0	9.6	10.2	10.8	11.4	12.0
V. conspersa	1	11	15	23	4	4				
V. papilionacea				3	12	11	13	18	13	1
hybrid, (C×P)		2	4	12	9	14	6	2		

Mean diameters = *conspersa* 8.1μ; *V. papilionacea* 10.1μ;
V. conspersa×*V. papilionacea* 9.0μ.

The above figures are based on measurements of approximately fifty nuclei of each species taken directly from the stained sections with the aid of an ocular micrometer as had been done with the cell lengths. Though the majority of nuclei were spherical those which were elliptical in shape were measured on both their short and long axis and the average recorded. No fractions under one half a micron were included in the data. Due to the rather small range of size variation in the diameters measured, this number of measurements was considered to be fairly representative. As in the former sets of figures, the weighted mean was computed for each series. It is apparent that these mean nuclear diameters do not vary much from the modal class.

From the mean diameters given it can be seen that there is a percentage difference in nuclear size of approximately 20% between the two parents and that the mean diameter of the hybrid nuclei lies almost mid-intermediate between the two parents. That is, the hybrid nuclei seem to be ten percent larger than those of *V. conspersa*, and ten percent smaller than those of *V. papilionacea*.

III. Chromosome Measurements

The chromosome number of the two parents is quite different (*V. conspersa* 2n–20, *V. papilionacea* 2n–54) while the hybrid plants display a number (2n–37) which, as might be expected, is the sum of the haploid number from each parent species. Not only is there a rather marked difference in chromosome number between the two species, but there is also a very marked difference in chromosome size. Careful measurements of the somatic chromosomes were taken in both parents and the hybrid to determine if possible whether these characteristic size differences were truly persistent in the cells of the hybrid

In view of the fact, recently emphasized anew by Navashin (1934), that chromosome size varies in different individual plants of the same species and probably from tissue to tissue of the same individual, it was considered essential to measure chromosomes that were comparable as regards their origin. Navashin (loc. cit) found that the chromosomes measured in mature roots displayed a range of size that was considerably larger than in embryonic roots. In a similar manner, Gershoy (1934) has observed that the chromosomes found in the vacuolated cells of the young flower bud tissue of different violet species show a tendency to be somewhat smaller than in the cells of the root tip. For this reason, therefore, the equatorial plates selected for measurement were all taken from: (1) mature roots; (2) in all but a few cases from the periblem of the root; (3) from the most actively dividing region just back of the growing point.

In spite of the precautions noted above, of selecting equatorial plates only from comparable regions of the root tip (as is noted in the graphs shown below of the classes of chromosome lengths in different cells of the same species) the range of size varies greatly from cell to cell. Even more significant is the fact that the individual sizes show an irregular distribution of lengths from cell to cell, an irregularity which in most cases is not even relatively comparable. To point out a striking example, in figure 2, curve III of *V. conspersa* shows eight chromosomes out of the diploid number of twenty ranging from 2.72μ to 3.84μ in length. In curve II directly beneath it, it is quite apparent that there are no chromosomes that equal in length even the shortest of the eight chromosomes which were present in curve III. In other words, none were longer than 2.5μ and most were considerably shorter. This is true in spite of the fact that the chromosomes were taken from cells which were in the same tissue of two tips which had been sectioned and stained simultaneously. The criticism might well be suggested that in spite of the similar treatment given to both tips, for some reason the chromosomes of curve II are simply more condensed than those of curve III. Yet even a glance at the two curves will show that they are not even *relatively* comparable whether in total range or in the different peaks shown. In fact a careful examination of the different curves (fig. 2) plotted for *V. conspersa* indicates that only two curves (I and II) seem at all comparable as regards the relative class distribution of chromosome lengths, and in both of these the range of size is quite different.

For a further analysis of these data curves II and III of the hybrid may be considered. It is to be noted that the curves were taken from periblem cells in both cases and that furthermore the curves are comparable as regards total range of chromosome lengths. Nevertheless,

curve III contained four chromosomes ranging in size from 1.92μ to 2.4μ whereas curve II showed no chromosomes in the same range of size. Apparently in the formation of chromosomes from the discontinuous spireme the chromatin condensed into smaller units or chromosomes about 1.28μ long, as is indicated by the peak at the left (II). It would seem that any attempt to identify all the members of the diploid complement from

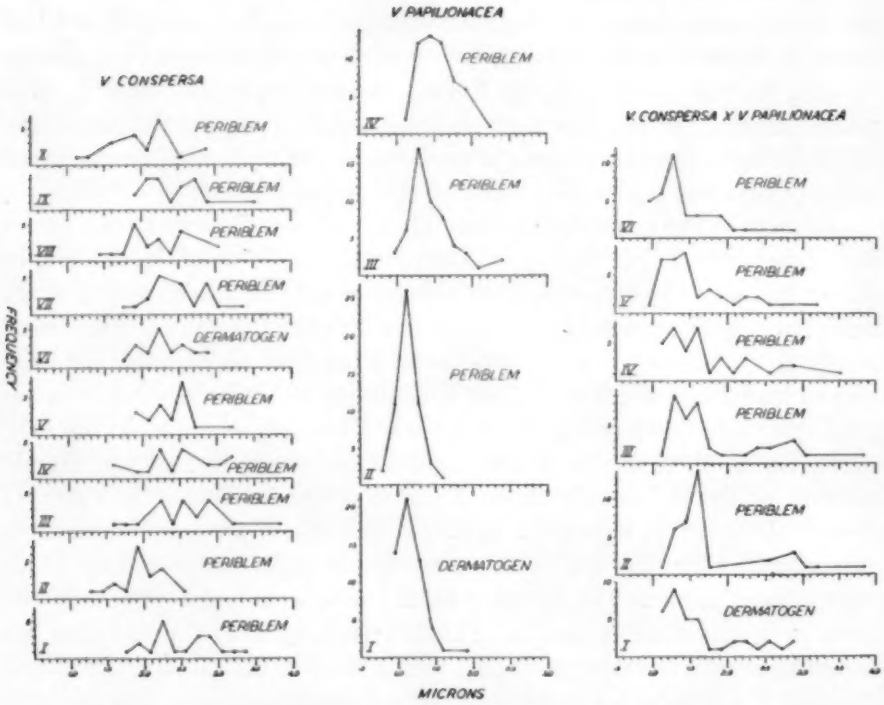


Fig. 2. Graphical curves showing the distribution of chromosome lengths of representative cells of the two parent species and the hybrid. (In each case the tissue from which the chromosome plate was drawn, is noted.)

cell to cell, on a basis of even comparable relative chromosome length, in this violet material at least, is extremely difficult.

The chromosomes from several cells of the epidermis have been measured to compare their sizes with those in the cells of the periblem. The curves shown on the chart indicate at least in the few cells measured, that chromosome sizes in the epidermis seem to be comparable to the smaller of the chromosome sizes found in the cells of the periblem. This would seem to agree with the observation made above (i.e., the epidermal cells appear to be smaller than the largest of the periblem cells). It should be

borne in mind, as pointed out above, that although the measurements plotted graphically are comparable, in some cases at least they are less than the actual chromosome lengths because of the foreshortening resulting from the position of the chromosomes on the equatorial plate. Any statement regarding the relation, if any, between cell size and chromosome sizes, would obviously require much more evidence.

The curves shown on the graph in figure 3 represent the frequency distribution of all chromosomes measured in the two species and the hybrid. A total of approximately 300 chromosomes were measured in each species,

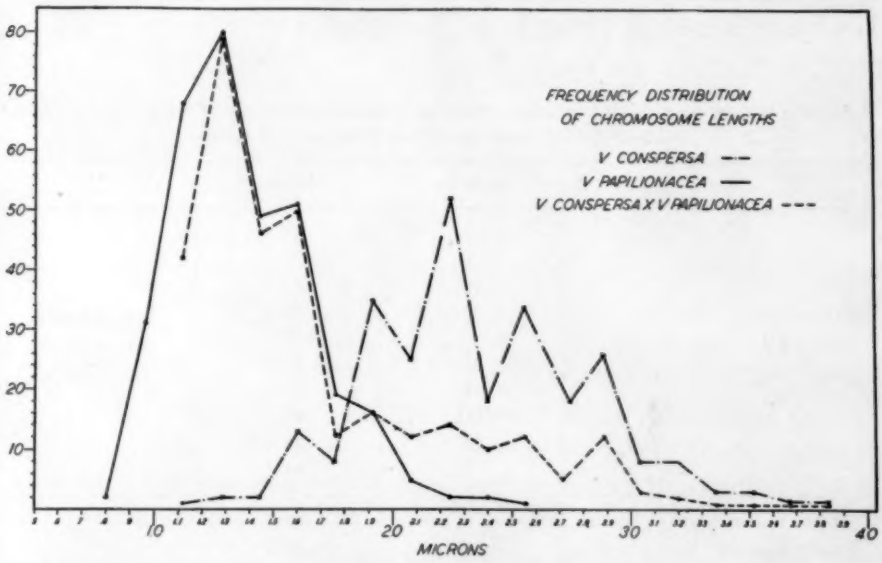


Fig. 3. Frequency distribution of total chromosome measurements taken in each species and the hybrid. (Approximately 300 in each case.)

a number which in a graphical curve obviously smooths out the individual difference noticeable in any single plate. It is apparent that the two parents each show fairly symmetrical curves of frequency distribution with a definite and characteristic peak, or modal class. The hybrid, on the other hand, shows a bimodal curve as regards the range of lengths with one modal class clearly defined and corresponding to modal class of the pollen parent *V. papilionacea*. Another peak, not as clearly defined, tends to be approximately .3μ smaller than the corresponding peak of the seed parent *V. conspersa*. Examination of the curve of *V. papilionacea* discloses the fact that 33 chromosomes of the genus (the first two points from left to right) are .96μ or less in length, while none of those measured in the hybrid cells were as small. In a comparison of the curve of the seed parent *V.*

conspersa with the curve of the hybrid it becomes apparent that if the longest of the hybrid chromosomes are as long as the longest of those of *V. conspersa*, the majority of them show a distinct tendency to be smaller. This apparent tendency for small chromosomes of the pollen parent to become larger and of larger chromosomes of the seed parent to become smaller in the hybrid cell is analogous to the condition found by Navashin in some of the hybrids between species of *Crepis*, which had different chromosome sizes in either parent. He has given the term neutral amphiplasty to this neutral, reciprocal influence in the hybrid in which the whole chromosome complement of either parent seems to be affected under the new conditions which obtain in the hybrid cell.

TABLE 4

Differences between the absolute total lengths of the diploid chromosome sets of the two parent species and their hybrid. From adult roots (compare with fig. 2).

PLANT	PLATE NO.	MICRONS	
V. conspersa (2n=20)	I	49.0	Min.—39.3 Ave.—46.9 Max.—50.6
	II	39.3	
	III	51.2	
	IV	50.6	
	V	47.9	
	VI	46.9	
	VII	50.3	
	VIII	44.3	
	IX	48.8	
	X	41.1	
V. papilionacea (2n=54)	I	63.3	Min.—61.7 Ave.—71.9 Max.—84.1
	II	61.7	
	III	78.5	
	IV	84.1	
V. conspersa×*V. papilionacea* (2n=37)	I	61.7	Min.—54.6 Ave.—62.6 Max.—67.7
	II	67.5	
	III	67.7	
	IV	65.6	
	V	59.1	
	VI	54.6	

(In the above table the figures opposite the Roman numerals merely represent the summation of the measurements of the chromosomes from that particular equatorial plate. The Roman numerals refer directly to the frequency curves plotted on the graph of figure 2.)

A tabulation of the total chromosome lengths in several cell plates, given in table IV, is of interest. It is to be noticed that there exists here, as in other measurements, a rather wide range of total chromosome lengths

from cell to cell, least in the hybrid and greatest in *V. papilionacea*. The computed average, underlined in the table, indicate a fairly close correlation with another possible measure of chromatin mass, namely nuclear volume. Furthermore, there is also a correlation on the one hand between chromatin volume measured by both methods and chromosome number, and cell volume on the other.

TABLE 5

SPECIES	CELL				NUCLEUS		N/C RATIO
	RANGE	CROSS SECTION AREA SQ. MICRA	LONGITUD. DIMENS. MICRA	COMPUTED CELL VOL. CU. MICRA	DIAMETER MICRA	COMPUTED NUC. VOL. CU. MICRA	
V. conspersa	Min.	83.2	6.3		6.6		
	Mean	210.9	10.8	2277.7	8.1	268.1	1:7.4
	Max.	370.4	19.2		9.6		
V. papilionacea	Min.	83.2	8.4		8.4		
	Mean	229.8	15.7	3607.8	10.1	523.6	1:5.8
	Max.	423.3	22.8		12.0		
Hybrid	Min.	75.6	7.2		7.2		
	Mean	214.3	12.8	2743.0	8.6	333.0	1:7.2
	Max.	370.4	21.6		10.8		

The above composite table presents at a glance the cardinal points in the range of the cell and nuclear measurements taken. It also shows the computed cell and nuclear volumes for the cells of the epidermis of the two parent species and the hybrid, as well as the nucleo-cytoplasmic ratios computed from the mean cell and nuclear volumes. These compare very closely with ratios given by Klieneberger (1918) for tissue of the root tip meristem of different genera.

DISCUSSION

An analysis of the above data, in the light of the current literature, touches upon several problems of theoretical interest. It seems that the karyotype is not fixed and unvarying in form, but rather as Navashin (1934) and others have shown [Delaunay (1931), Kagawa (1929)] that it is subject to environmental as well as to inherent alterations occurring in the ontogeny of an organism. Aware of this fact, the writer has taken precautions mentioned above, to select root tips grown under uniform conditions as well as to subject them to a similar treatment in preparation for staining. The measurements of chromosome plates were taken from cells which were in most cases from comparable regions of the same tissue of the root.

The following question at once presents itself: is the occurrence of marked differences in total chromosome lengths and the even more, apparently, fortuitous distribution of individual chromosome lengths from cell to cell compatible with the theory of chromosome individuality in the sense of genic and chromomeric make-up? In spite of the rather marked differences in total range as well as distribution of chromosome lengths in comparable cells of the same species, a comparison of approximately 300 chromosomes from each parent and the hybrid shows that there has occurred an alteration in the hybrid, at least as regards the chromosome lengths of its parental haploid complements. This condition noted in the chromosomes of the hybrid cells, called "neutral amphiplasty" by Navashin, seems to indicate that the hybrid consists of cells and formed cytoplasmic components which, together with its chromosomes, are not characteristic of either parent alone but rather of the hybrid organism. There is suggested the occurrence of an interaction of two different protoplasms, from fertilization to physiological maturity. A preliminary study of flower buds produced late this year indicates that not only is the flower bud formation delayed, but that the maturation divisions in all but a few buds do not progress beyond the prophase of the first division.[3] Bold and Gershoy (1934) have pointed out in connection with studies made on other sterile species hybrids, that despite the apparent vigor of the hybrid organism the disturbed cell and nuclear relations are not limited to the spore tissue alone but are indicated elsewhere by the almost complete breakdown in differentiating tissue which may occur at various stages of flower bud formation, and usually previous to the maturation division in sporogenous tissue. It is here suggested that when statistically considered, the apparently haphazard size-distribution of the individual chromosomes of a complement from cell to cell in the same tissue of a given species, would probably be found to be the normal condition if a sufficiently large number of measurements were taken.

Even a cursory analysis of the literature regarding the importance of the individuality of form and size of the chromosomes, in relation to the expression of a definite morphology in the organism, reveals conflicting points of view. Navashin (1934), in discussing the views of earlier authors, quotes Morgan, Sturtevant, and Bridges, who say that "not the shapes and sizes of the chromosomes" are important "but the genes contained

[3] Subsequent studies of more fully developed flower buds showed complete asynapsis, along with the highly abnormal meiotic divisions characteristic of this type of sterile, violet species-hybrid. Such erratic and abortive reduction divisions in other sterile species-hybrids have been described earlier (Bamford and Gershoy, 1930; Bold and Gershoy, 1934).

in them." Yet, as Navashin points out, "this formula . . . cannot satisfy because the 'unimportant' sizes and shapes of the chromosomes are the only so far visible characteristics of the carriers of the genes" . . . "we would never guess the existence of genes unless we observed their developmental characteristics." He stresses the fact, moreover, that these characteristics can only be inferred from the chromosomes as we see them. It would seem to follow that a high degree of constancy in shape and size is necessary for the validity of the gene theory.

The conclusion of Navashin that the chromosomes are not "absolute things" but are rather influenced somewhat by the surrounding cellular medium is apparently borne out by the present investigation. Navashin, however, apparently does not consider the variation in chromosome sizes, which he has found, to be of such a magnitude as to conflict with the general idea of chromosome individuality. Yet the present writer is of the opinion that if evidence is presented for the occurrence of neutral amphiplasty and the presence of an appreciable range in variation in chromosome size from tissue to tissue, or even within the same tissue, the data should show that the variability is at least comparable. That the measurements here presented do not show evidence for the existence of even comparable variation in the distribution of chromosome length from cell to cell, particularly in the periblem of the root meristem, is quite obvious and significant. The data suggest rather that the chromatin of the nucleus, in its normally recurring cycle of condensation, accompanying the formation of chromosomes as discrete units and alternating with the diffusion and redistribution in the so-called metabolic phase, reappears as units which may express in somewhat haphazard fashion the same size-and-form range.

The evidence for the existence of a definite and constant chromosome individuality, similar to that found by Wenrich in the chromosomes of *Phrynotettix*, seems rather scanty (Sharp, 1934). In the diploid hybrid genom here studied there is no complete retention of the size characteristics of the haploid sets of the parents nor do they show a complete merging of size characteristics, as might perhaps be expected. Although the longer chromosomes of *V. conspersa* tend to become shorter and the shorter chromosomes of *V. papilionacea* parent tend to become longer in the hybrid, the chromatins of the two parents nevertheless do display an individuality of organization as species characters, expressed in the range of distribution in chromosome length, characters which are not entirely lost in those chromosomes which make up the hybrid genom. It may of course be possible but rather difficult to show in most species that the chromosomes never lose their individuality even in the resting phase, but

do become vesiculated as various investigators mentioned above have postulated. The evidence for the maintenance of chromosome individuality in the form of vesicles exists only in scattered instances. But the inference is still current that an individuality of some sort persists from one division to another.

A much simpler hypothesis might perhaps be advanced, namely, that a very slight difference in chemical composition of the chromatin of either parent would tend to keep the two separate, thus accounting in the hybrid genom for the persistence of species characteristics.

From the data presented here and by Marvin (1936), and from the evidence brought forth in the literature on the problem, the direct relation of cell size to morphogenesis is not clearly established. Less tangible is the bearing of the nucleo-cytoplasmic ratio on form development in the many celled organism. That the size and form of the chromosomes as such, are directly concerned with differences in morphological expression, is by no means established, although the indirect evidence secured from the vast data of genetical studies definitely assumes such a direct relationship.

The data, in the violets at least, indicate that a more intensive biometric study of the normal range of variation in chromosome size and shape is a necessary prerequisite of one critical approach to the fundamental validity of current cyto-genetical assumptions.

This study was carried on under the direction of Dr. A. Gershoy, to whom I am indebted for many helpful suggestions and criticism as well as for the use of his pedigreed stock. In addition I wish to express my gratitude to Professors G. P. Burns, B. F. Lutman, and R. A. Harper for criticism of the manuscript.

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An abnormal method of branching

P. A. Davies

(with plate 5 and two text-figures)

An abnormal method of branching occurs at the apex of many rapidly growing shoots of *Ailanthus altissima* Swingle. The writer, during the past three seasons (1932–1934), has found 204 cases of this method of branching. It is so unusual and so different from the normal method of branching that its structure and ontogeny is of interest.

The normal method of branching in *Ailanthus* is forked and irregular, with shoots developing at irregular intervals along the mother shoot (pl. 5, fig. A). The large pithy area in the center of the mother shoot is not continuous with the pith of the branch; an intervening area is occupied by the wood (pl. 5, fig. B). The abnormal method of branching, which appears at the apex of the mother shoot, is fan-shaped and flattened (pl. 5, figs. C and D). The pith of the mother shoot is continuous with the pith of the branches and no intervening areas of wood appear.

Shoots in the normal method of branching arise from buds which developed the previous season. These buds form in the axils of the leaves, so the position of the leaves on the stem determines the position of the new shoots. If all the buds developed into shoots, the shoot arrangement on the mother stem would be as symmetrical as the leaf arrangement; but not all the buds develop, so the branching presents an irregular pattern.

Theiss,[1] studying 661 mother stems of *Ailanthus*, found that the number of shoots on a stem varied from 1 to 8, with an average of 2.24. The abnormal method of branching occurs at the apex of rapidly growing shoots, and its growth and position are not dependent on bud formations of the previous seasons, but is the result of an abnormal distribution of leaves on the shoot of the current season's growth. The position of the shoots in both the normal and the abnormal methods of branching depend on leaf position; the normal on leaf position of the previous season's growth and the abnormal method on leaf position of the current season's growth. An understanding of leaf position is important in understanding the cause of this peculiar method of branching. The normal leaf arrangement or system in *Ailanthus* is octostichous or eight-ranked. The angular divergence of the leaves is 135° or three-eighths of a circumference. In such an arrangement, with the completion of the third revolution, leaf number nine is in position in line with leaf number one. Wright (1867) points out that in this type of arrangement the leaves are distributed

[1] Theiss, E. W. 1933. Factors affecting the method of branching in *Ailanthus altissima*. Unpublished thesis. Univ. of Louisville.

most thoroughly around the stem, exposed most completely to light and air, and provided with the greatest freedom of symmetrical expansion, together with a compact arrangement in the bud. The regular distribution maintains the normal symmetry of the stem. In the abnormal method of branching, the lower part of the mother shoot has the normal three-eighths leaf arrangement and the normal symmetry. At the apex of the mother shoot, the normal leaf arrangement is destroyed and the leaves appear in an abnormal arrangement (pl. 5, figs. C and D). With the completion of the third revolution, leaf number nine is not in line with leaf number one. When the symmetry of the shoot has been destroyed to such an extent that it flattens at the apex, the peculiar method of branching appears.

In any season, the normal shoot growth in *Ailanthus* is of two types: (1) short spur-like shoots (pl. 5, fig. A), which are rarely more than eighteen inches long; and (2) long shoots, which may reach more than sixteen feet in length. The spur-like shoots are found on older trees, which because of extension growth, produce many but short shoots. The spur-like shoots on the upper part of the tree generally terminate in flower panicles. The long shoots on young rapidly growing trees, which produce few shoots, often only one, never terminate in flower panicles. The spur-like shoots (slow-growing shoots), as far as observations have been able to determine, produce only the normal leaf arrangement and the normal symmetry. In the long shoots (rapidly growing shoots) the normal leaf arrangement at the apex is the rule, but exceptions in the form of abnormal leaf arrangements occur, which may result in a flattened stem.

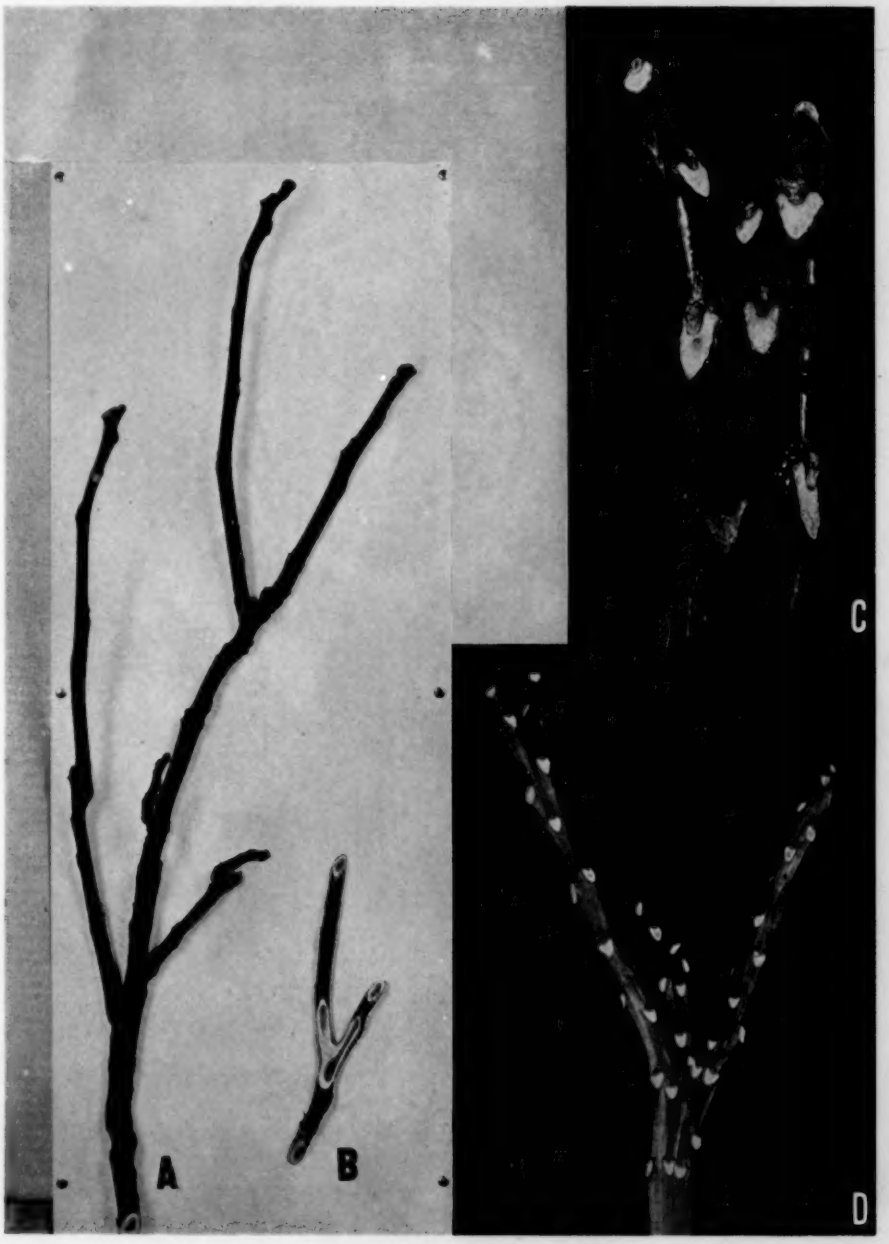
As the abnormal method of branching is found at the apex of rapidly growing shoots, and as it is the result of an abnormal arrangement of leaves on the shoot, it appears that rapidity of growth is an internal correlatory factor in determining the position of the leaf primordia at the rapidly differentiating shoot apex in *Ailanthus altissima*. Evidence is at hand to support the statement that internal forces play a rôle in determining leaf position. Winkler (1901, 1902) states that inner correlations along with heredity and outside influences determine leaf arrangement,

Explanation of plate 5

Fig. A. A tip of one of the main branches of a large tree. The method of branching is forked and irregular.

Fig. B. Normal branch with part of the wood cut away so as to show the union between the branch and the mother stem. The pith of the branch is not continuous with the mother stem.

Figs. C–D. Apices of rapidly growing young shoots which have flattened and are in the process of branching. Distinct growing centers may be observed. Leaf scars indicate the position of the leaves.



DAVIES: ABNORMAL BRANCHING

and that no single factor plays an important rôle in all types of leaf arrangement. Schwendener (1901) states that pure mechanical causes (internal forces) acting at the place of origin determine leaf arrangement.

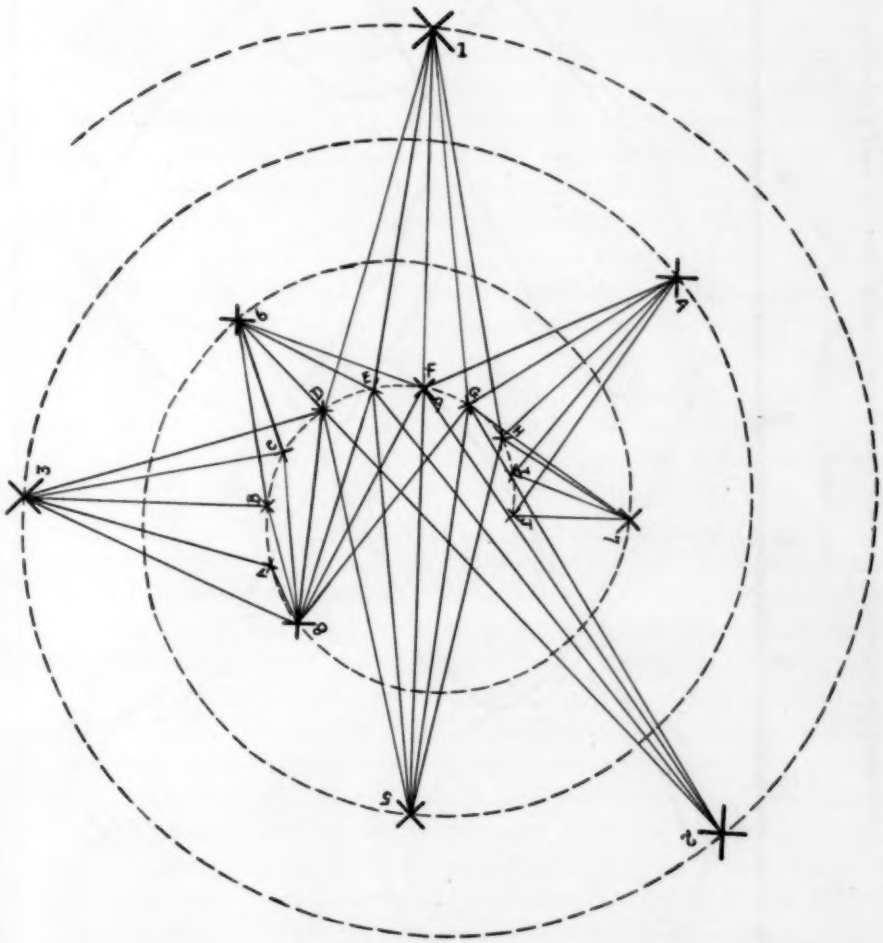


Fig. 1. A diagrammatic representation of a complete cycle in the normal three-eighths leaf arrangement. Crosses marked 1, 2, 3, 4, etc., represent developing leaf primordia. Crosses marked A, B, C, D, etc., are assumed positions of leaf primordia. The straight lines drawn from the developing leaf primordia to the assumed primordial positions represent the extent of influence the developing leaf primordia have over the assumed primordia. The shorter the line the greater the influence.

Foster (1928) says that evidence at hand suggests that the leaf primordia at the growing apex are genetically multipotent and hence capable of developing along a number of lines which are secondarily determined by

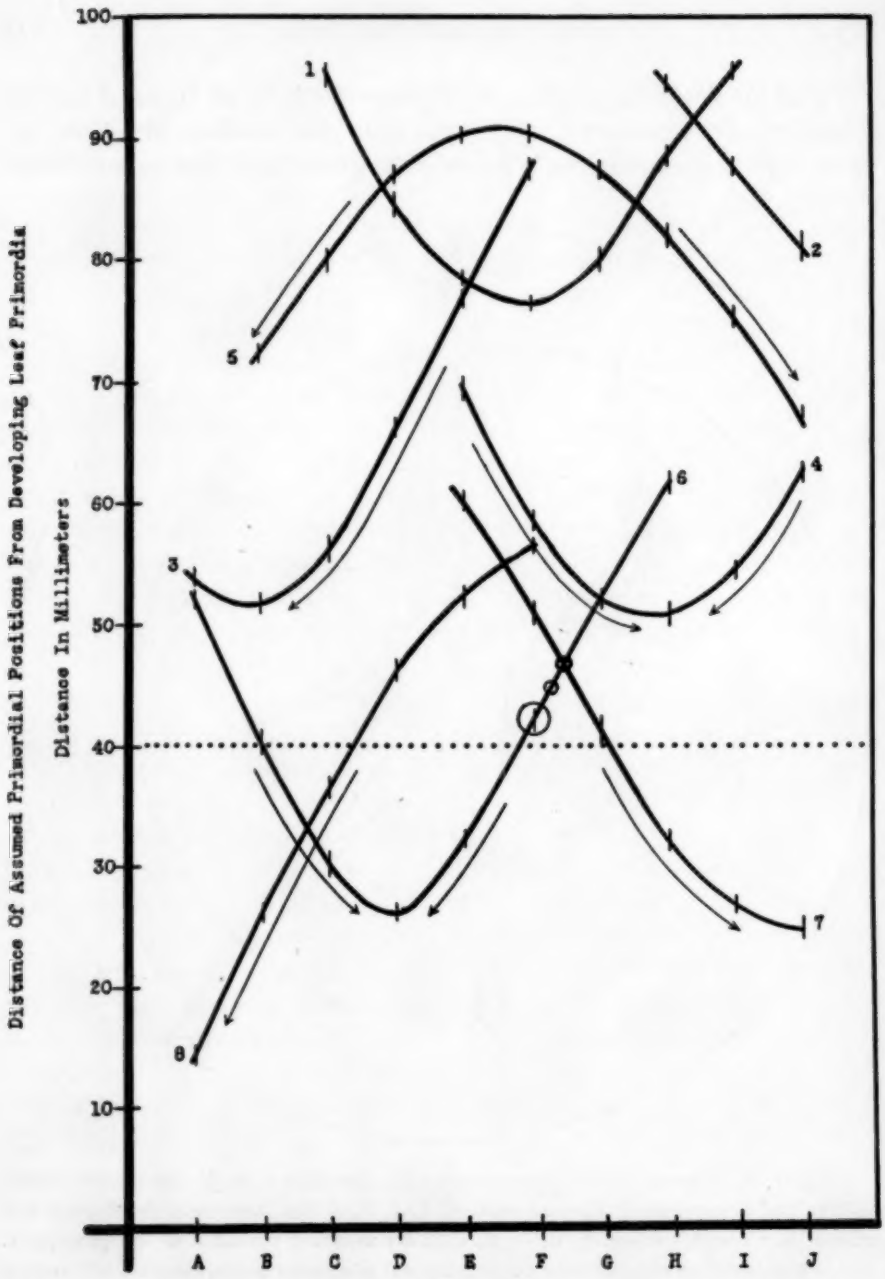


Fig. 2. A graphic representation of the data given in fig. 1. Each curve represents the influence that a developing leaf primordium has on the assumed primordia. The arrows indicate the direction of increasing influence. The large circle indicates the position of the developing normal ninth leaf primordium relative to the extent of influence exerted by the developing leaf primordia.

external and internal forces, and the relation of the growth initial to the shoot as a whole.

Figure 1 is a schematic arrangement which illustrates the relative position of the leaf primordia in a complete cycle in the normal three-eighths leaf arrangement. The spiral is viewed from the apex of the shoot. The leaf primordia in the outer part of the spiral are older. Leaf primordium 1 is the oldest and farthest down the shoot, while leaf primordium 9, at the apex, is the last one formed. Crosses marked A,B,C, D,E,F, etc., are assumed positions where leaf primordia might develop from the undifferentiated tissue at the apex of the shoot. Assumed leaf primordial position F is the position of the primordium which normally develops into the ninth leaf and completes the cycle. The lengths of the straight lines drawn from the developing primordia to the assumed primordial positions represent the extent of influence (dominance) that the developing leaf primordia have on the undifferentiated tissue at the apex of the shoot. The shorter the line the greater the influence.

Figure 2 shows a graphic representation of the data given in figure 1. Each curve represents the dominance, indicated by the length of the lines in figure 1, that a developing leaf primordium has on the assumed leaf primordia. The arrows indicate the direction of the greatest influence. The large circle indicates the position (assumed position F) of the normal ninth leaf primordium relative to the extent of influence exerted by the developing leaf primordia. The dotted line indicates the extent of the dominating influences of the leaf primordia on the assumed primordial positions. Below the dotted line, the dominating influence is great enough to prevent the development of a leaf primordium in the assumed positions; while above the dotted line, the influence is not great enough to prevent the development of leaf primordia in the assumed positions. The influence of leaf primordium 8 is sufficient to prevent the development of a new one in assumed position A. The combined influence of 8 and 6 is sufficient to prevent new ones from developing in assumed positions B and C. The influence of 6 is sufficient to prevent the development in assumed position D and E, but the influence is greater at D than at E. At the assumed position F, just above the dotted line, the position at which the normal ninth leaf develops, the influence of combined existing leaf primordia is not great enough to prevent the development of a normal leaf primordium in this position. The newly formed ninth leaf primordium matures to such an extent that it exerts a dominating influence sufficient to prevent the formation of a new one in assumed position G. The combined influence of of 9, 7, and 4 is sufficient to prevent the formation of primordia in assumed positions H, I, and J. Not until a position is reached, above leaf pri-

mordium 2, where a decrease of influence similar to that exerted at position F, will another normal leaf primordium develop. In the abnormal method of branching, growth is so rapid at the apex of the shoot that additional leaf primordia (indicated by the small circles) are formed in close proximity to the ninth leaf primordium before it can mature sufficiently to exert an influence preventing the development of additional leaf primordia. Multiple development may continue until the influence of leaf primordium 7 or the cessation of rapid growth so that the last formed primordium can mature sufficiently to exert a controlling influence, stopping the multiple development. Another one will not be formed until a position is reached where the lowering of the influence is sufficient to allow a new leaf primordium to develop, and this new one will be out of normal position. When they develop out of the normal position, they destroy the normal symmetrical leaf arrangement above that point. The abnormal arrangement of leaves results in an unequal demand for conducting tissues. If the leaves occur in opposite groups on the shoot, opposite increases of conducting tissues will result. This opposite growth will result in a flattened shoot. If the shoot becomes very flat toward the apex, the intervening areas between the growing centers split. The separating of the growing centers result in the abnormal method of branching.

SUMMARY

An abnormal method of branching occurs at the apex of many rapidly growing shoots of *Ailanthus altissima*.

An abnormal distribution of leaves occurs. This results in a flattened stem apex with definite growing centers. The intervening areas between the growing centers split, resulting in the abnormal branching pattern.

An explanation of the process is given.

DEPARTMENT OF BOTANY
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New and noteworthy trees in Texas and Mexico

C. H. Mueller

In July, 1933 an elm lacking fruits was collected and repeatedly observed in the Sierra Madre Oriental in Diente Canyon about twelve miles south of Monterrey, N. L., Mexico. It was found commonly scattered in two deep, moist, and wooded arroyos ranging from 3,000 to 5,000 feet in altitude where it grows in association with *Tilia*, *Cercis*, and several oaks.

The vegetative characters very strongly suggest *Ulmus americana* L. to which it is apparently closely related. Standley writes,[1] "Sessé and Mociño reported (Pl. Hisp. 45. 1887) *Ulmus americana* from Mexico. The plant (if the report is based on an actual plant) probably belongs to some other genus." It seems reasonable to believe that Sessé and Mociño might have encountered in vegetative condition the species here described as new, for it was not until the collection of fruits in May, 1934 that critical characters distinguishing it from *U. americana* could be recognized beyond doubt.

The collection of fruits was not accomplished without difficulty, for the time of fruiting is evidently in very early spring, and hardly any but fallen fruits and peduncles which were lodged in debris-filled crevices could be found. That these were not dropped the autumn before was clearly indicated by the occasional finding of fruits lodged in comparatively fresh and fragile spider webs which could hardly have survived the winter intact in their unprotected situations.

The species differs from *U. floridana* Chapm. in its bristle-clothed leaves and short petioles. It may be distinguished from *U. alata* Michx. by its merely ciliate samara wings and hispidulous leaves. It differs from *U. fulva* Michx. in its ovate samara with the wings glabrous save for the ciliate edges. From *U. americana*, to which it is closely related, it differs in having the tips of the samara widely divergent and quite indurated. Mr. Paul C. Standley, to whom some vegetative specimens were submitted suggested the possibility that the species might prove distinct if the fruits were known. The character of the persistent styles or samara tips suggests the name *Ulmus divaricata*. A description follows:

Ulmus divaricata C. H. Muell. sp. nov.

A small tree usually about 10 m. tall with a trunk diameter of 30 cm. or less and moderately but rather finely furrowed, dark brown bark in thin,

[1] Contr. U. S. Nat. Herb. **23**: 198. Standley credits only *U. crassifolia* Nutt. to Mexico and that by the inference that it must cross the Rio Grande from the Texas border country where it is common.

narrow plates. Branches long and gracefully spreading. Twigs round, very slender (0.6 to 2 mm.), reddish brown, rather densely pubescent with short, silky hairs, becoming glabrous during the second year and acquiring a few light gray, rather inconspicuous lenticels (or light brown, conspicuous ones in the case of very vigorous shoots). Buds brown, conical, decidedly acute, about 1×2–2.5 mm. with a pair of awl-like stipules about 5 mm. long usually persistent. Leaves broadly lanceolate to sub-ovate, twice serrate with acute, somewhat mucronate, incurved teeth, inequilaterally somewhat auriculate at the base, moderately small (1–3.5×3.5–8 cm.) or on vigorous shoots broader, long attenuate at the apex, narrow at the base, and moderately large (as large as 7×14 cm.); the two surfaces roughened by very stiff, short hairs sparsely distributed and not readily visible; midrib and veins slightly impressed above and prominent beneath with short, dense, silky hairs; petiole short (0.5–1.5 ×2–5 mm. depending on the leaf size), brown, and densely soft-pubescent like the midrib. Flowers vernal (by inference). Fruiting peduncles 20–25 mm. long bearing 5–8 pedicels 6–8 mm. long which bear thickened nodes well above the middle as though there might earlier have been bractlets. Fruit falling from the pedicel before the deciduous peduncle; samara ovate to obovate, about 3–5×5–8 mm., deeply notched at the apex, the styles broadly divergent or rarely merely erect, 1–1.5 mm. long, indurated and usually finely tapered; the wings margined by a heavy vein, glabrous except for being densely ciliate strictly on the edges. (Not every specimen exhibits this character plainly; on some the hairs are extremely short, and on others apparently the material has been somewhat damaged by exposure to the weather. It is quite distinct on most of the better preserved specimens, however.)

Ramuli graciles, annotini dense breviterque pubescentes; gemmae conicae acutae, circiter 2–2.5 mm. longae 1 mm. crassae, stipulis subulatis circiter 5 mm. longis plerumque persistentibus; folia ex late lanceolatis fere ovata, 3.5–8 cm. longa, 1–3.5 mm. lata, duplo serrata, basi inaequilateraliter subauriculata, utrinque pilis brevibus rigidis asperata, venis supra impressis, subtus prominentibus pilis brevibus confertis sericeis; flores vernales; pedunculi fructiferi 20–25 mm. longi; pedicelli 5–8, 6–8 mm. longi, ulta medium nodosi locum bractearum indicantes; samarae ex ovatis obovatae, circiter 5–8 mm. longae 3–5 mm. latae, apice alte retusae, stylis induratis late divergentibus aut rare erectis; alis glabris marginibus dense ciliatis exceptis.

The types [C. H. & M. T. Mueller no. 62 (vegetative) collected July 4, 1933 and no. 251 (fruit from the same individual tree) collected May 6, 1934, in Diente Canyon about 12 miles south of Monterrey, N. L., Mexico] are deposited in the herbarium of the Arnold Arboretum at Jamaica Plain, Mass., and in the author's herbarium at Cuero, Texas. The herbarium of the New York Botanical Garden contains a co-type. The herbaria of the Field Museum of Natural History at Chicago and the University of Texas at Austin contain vegetative specimens of which no. 61—1933 is atypical

in that it consists of vigorous shade branchlets with abnormally large leaves.

In a collection of plants made in July and August, 1933 in and about Diente Canyon of the Sierra Madre Oriental about twelve miles south of Monterrey, Nuevo Leon, Mexico, by the author and Mary Taylor Mueller there were found ten species and eight forms of oaks. Of these five species and two forms have been identified as follows by Dr. Wm. Trelease and the author: *Quercus polymorpha* Cham. & Schl., *Q. fusiformis* Small, *Q. Muehlenbergii* f. *Alexanderi* (Britton) Trel. (?), *Q. Standleyi* Trel., *Q. rysophylla* Weatherby, *Q. Canbyi* Trel., and *Q. Canbyi* f. *adscendens* Trel. The form here referred to *Q. Muehlenbergii* f. *Alexanderi*, although it may not quite fit the form, represents a considerable though not unexpected extension of the range of the species. *Q. Muehlenbergii* Engelm. is found in the mountains of western Texas and New Mexico.[2] *Q. Standleyi* was known previously only from the Sierra Madre Occidental.[3] This collection adds considerably to its range. The remaining forms could not be placed critically and are here described as new.

A more recent collection in more southerly localities of the Sierra Madre Oriental promises to yield many additional facts of distribution and relationships of some of these species. This collection will be described later as time permits.

The types of the species described below are deposited in the herbarium of the University of Illinois at Urbana. Series of co-types (named in the order of completeness) are preserved in the Mueller Herbarium at Cuero, Texas, the herbarium of the University of Texas at Austin, and the herbarium of the University of Mexico in Mexico City.

Quercus clivicola Trel. & Muell. sp. nov.
(Leucobalanus—Glaucoideae)

Twigs rather slender (2–3 mm.), somewhat fluted, rusty-tomentulose for a time, becoming gray with rather conspicuous lenticels. Buds globose and gray becoming ovoid and 2×3 mm., the upper accompanied by long setaceous stipules. Leaves elliptic-oblong, broadly acute or sometimes obtuse, cordate, entire or somewhat undulate upwards, narrowly revolute, 2–4×6–11 cm., dull, glabrous and minutely cancellate above, yellowish-subtomentulose beneath; veins some 10 or 12×2, looping; petiole tomentulose, scarcely 5 mm long. Staminate catkins about 40 mm. long, loosely flowered, the pistillate about 45 mm. long in summer with flowers apparently sessile and paired or in threes. Fruit annual, finally solitary or paired in groups on the tomentulose

[2] Wooton and Standley, Contr. U. S. Nat. Herb. **19**: 171.
[3] Trelease, Mem. Nat. Acad. Sci. **20**: 57.

peduncle; cups deeply saucer-shaped, 15 mm. or more in diameter, with obscurely keeled acute appressed scales gray or brown when glabrate; acorns ovoid, scarcely 14×16 mm., rather loose in the cup, striately pubescent in the depressed end.

Ramuli juvenes ferrugineo-tomentulosi; folia elliptico-oblonga acuta basi cordata vix aliquanto undulata, 2–4×6–11 cm., infra flavicante-tomentulosa; petiolus tomentulosus, brevis; fructus annui, solitarii vel geminati, peduncule 4–5 cm. longo; glans ovoidea, basi, sublaxe inclusa.

The type is C. H. & M. T. Mueller no. 584—1933. The fruits were distributed with no. 597—1933 under the name *Q. consanguinea* Trel. & Muell. which may be regarded as a shade form of *Q. clivicola* having much larger leaves and called f. **consanguinea** Muell. f. nov.

A small or moderate tree with somewhat gnarled branches and deeply furrowed gray bark. Common on the drier openly wooded slopes.

Q. clivicola is apparently most closely related to *Q. glaucoides* Martens & Galeoti:

Leaves quickly glabrate, lightly glaucous beneath; petioles glabrescent; twigs soon glabrous ..... *Q. glaucoides.*
Leaves densely short hairy beneath; petioles and young twigs densely pubescent ..... *Q. clivicola.*

Quercus clivicola f. **crenifolia** Trel. & Muell. f. nov.

Leaves more elongated-oblong, coarsely crenate, decidedly less pubescent beneath; petiole 7 or 8 mm. long. Pistillate catkins in summer about 50 or 60 mm. long, scurfy, several flowers at the end and about the middle sessile and singly disposed; the round cup with blunt scales, brown when glabrescent.

Folia elongato-oblonga; amenta fertiles 50 mm. longa, sursum pauciflora.

The type is C. H. & M. T. Mueller no. 585—1933.

Quercus clivicola f. **dentata** Trel. & Muell. f. nov.

Scarcely differs from the species except that many leaves become acutely and coarsely mucronate-dentate upwards, the petioles rarely exceed 3 mm. in length, the single young fruit observed is borne on a peduncle only 3 mm. long.

Differt foliis inferioribus sursum acute dentatis; petiolus 3 mm. longus.

The type is C. H. & M. T. Mueller no. 583—1933. No. 584a is to be referred here also.

Quercus microlepis Trel. & Muell. sp. nov.

(Leucobalanus—Glaucoideae)

Twigs slender (2 or 3 mm.), fluted, glabrous, gray-brown with numerous minute pale lenticels. Leaves deciduous?, hard-papery, oblong or occasionally subovate, obtuse, round-based or frequently somewhat cordate, entire or ex-

ceptionally shouldered near the end or mucronately toothed, 2–3×5.5–7 cm., bluish green, glabrous, flat or convallately cordate; veins about 10×2, looping; petiole slightly downy, scarcely 5 mm. long. Catkins? Fruit annual, usually paired on a pubescent stalk scarcely 5 mm. long; cup saucer-shaped, 15 mm. in diameter, pale-tomentulose with contrasting small brown tips; acorn oblong, about 9×20 mm., covered near the base only.

Folia oblonga, apice et basi obtusa sive obscure cordulata, aliquando sursum subundulata, 2–3×5–7 cm.; petiolus 5 mm. longus; fructus annui, in pedunculo breve binati; glans oblonga, cupula subplana.

The type is C. H. & M. T. Mueller no. 578—1933.

A moderate tree with wide spreading branches and moderately fissured gray bark. Sparse on the openly wooded lower slopes.

Q. microlepis is most closely related to *Q. glaucoides* Martens & Galeoti (?) or *Q. baldoquinae* Trel. (?):

Cup scales somewhat thickened.
Petiole glabrescent, 5 mm. long ..... *Q. glaucoides.*
Petiole glabrous or stellate fleecy above, 3 mm. long ..... *Q. baldoquinae.*
Cup scales thin, appressed, petiole slightly downy, 5 mm. long ..... *Q. microlepis.*

Quercus glaucophylla v. Seemen var. **macropetiolata** Muell. var. nov.

Rather densely branched, glabrous. Twigs slender (2 mm.), fluted, red-brown with minute pale lenticels. Buds round and blunt or ovoid and acute, some 2×2 or 3 mm., glabrate and brown, with setaceous stipules persistent above. Leaves deciduous?, blue-green and glabrous save for a few tufts of stellate hairs at the base of the midrib above, yellow granular, scantily stellate hairy and finely cobwebby with appressed simple hairs beneath, or entirely glabrate on both surfaces, chartaceous, obovate or subpandurate, undulately few-lobed upwards, obtuse at both ends, narrowly revolute, 2–3×4–5 cm.; veins about 8×2, fine but prominent on both sides, very venose; petiole rosy, 5–10 or even 15 mm. long. Catkins? Young fruit sessile, globose, with appressed brown scales.

Glabrata; folia obovata vel subpandurata, utrinque obtusa sursum parcelobata, 2–3×4–5 cm.; petiolus 5–10 mm. longus, rubescens; fructus sessiles.

This variety differs from the type chiefly in its pubescence and the length of its petioles.

The type is C. H. & M. T. Mueller no. 574—1933.

Quercus monterreyensis Trel. & Muell. sp. nov.

(Leucobalanus—Aurantiaceae)

Glabrate and very glossy. Twigs rather slender (2 or 3 mm.), fluted, gray with conspicuous pale lenticels. Buds subacutely ovoid, brown, glabrate, the terminal with persistent setaceous stipules. Leaves deciduous?, elliptic-sub-

obovate, subacute, obtuse or truncate-subcordate at base, entire or mostly coarsely crenate upwards, about 4×8 or 9 cm., gray- or olive-green above, yellow-olive and sparsely fleecy beneath; veins about 10×2, scarcely looping; petiole 5–10 mm. long, orange. Pistillate catkins subsessile, with several flowers finally reduced to 1 or 2. Fruit annual, solitary or paired on gray-brown sparingly fleecy stalks about 10 mm. long; cup deep-saucer-shaped, 15 mm. in diameter with closely appressed gray-tomentose thickened scales, short fringed; acorn ovoid, scarcely half included.

Glabrata, nitidissima; folia elliptico-obovata, subacuta, basi obtusa sive truncato-subcordata, integra vel sursum obscure crenulata, 4×8–9 cm.; petiolus 5–10 mm. longus; fructus annui, solitarii vel geminati pedunculo breve griseo; glans ovoidea vix semi-inclusa.

The type is C. H. & M. T. Mueller no. 596—1933.

A moderately small tree with deeply furrowed, dark gray bark. Infrequent in the dense pine-oak-hickory forest of a high canyon.

Q. monterreyensis differs considerably from all other species in the section Aurantiaceae:

Petioles 3–6 mm. long: the contracted leaf base somewhat rounded . . . . . *Q. Standleyi.*
Petioles 5 to usually 10 mm. long.
Leaves rather acute at the contracted base . . . . . *Q. aurantiaca.*
Leaves subacute to usually subcordate at the base which is scarcely contracted . . . . . *Q. monterreyensis.*

Quercus Canbyi f. **concolor** Trel. & Muell. f. nov.

Scarcely differing from f. *adscendens* except in its distinctly narrower leaves, 3 or 3.5×6 or 7 cm.

A f. *adscendens* differt foliis angustioribus, 3–3.5×6–7 cm.

The type is C. H. & M. T. Mueller no. 590—1933.

Quercus cupreata Trel. & Muell. sp. nov.
(Erythrobalanus—Acutifoliae).

Glabrous. Twigs slender (2 mm.), red-brown with minute pale lenticels, becoming gray with the lenticels more salient. Buds ellipsoid, acute, the scales ciliate and dark-margined, glossy, from reddish becoming clay-colored, 3×4 mm. Leaves narrowly lanceolate, aristately very acute, subcuneate, 3 or 4×10 or 12 cm., serrately lobed with long-setaceous points and U-shaped sinuses, dull blue-green and cancellate above, glossy copper-colored beneath; veins 8 or 10×2, alternately passing into the points of the lobes; petiole pink, slender, 25 or 30 mm. long. Pistillate catkins in summer 5–15 mm. long with 3–4 flowers singly disposed. Fruit biennial.

Glabra; folia anguste-lanceolata, peracuta, aristata, subcuneata, 3–4 ×10–12 cm., serrato-lobata dentibus longesetaceis, infra cupreata; petiolus gracilis 25–30 mm. longus; amenta fertiles subelongata sursum sub 3-floris; fructus biennis.

The type is C. H. & M. T. Mueller no. 586—1933.

A moderate tree with graceful, spreading branches and deeply fissured, dark gray or black bark. Abundant in the dense oak wood on one high slope.

Q. cupreata apparently is most closely related to *Q. Grahami* Bentham:

Leaves setaceously serrate, typically rounded at base, buds ovoid, 2×3 mm.....
.....*Q. Grahami.*
Leaves lobed with long-setaceous points, typically subcuneate at base, buds ellipsoid, 3×4 mm.....*Q. cupreata.*

Quercus cupreata f. **serrata** Trel. & Muell. f. nov.

Differs from the species in the lance-elliptic, less bronzed leaves, aristately serrate instead of lobed, with petioles about 10–18 mm. long.

Differt foliis verdescentibus lanceolata-ellipticis, minus profunde serratis, et petiolis brevioribus.

The type is C. H. & M. T. Mueller no. 595—1933.

Quercus runcinatifolia Trel. & Muell. sp. nov.

(Erythrobalanus—Acutifoliae).

Glabrous except for rather evident leaf domatia. Twigs reddish with minute white dots becoming small but prominent lenticels. Buds ovoid, acute, 3×4 mm., grayish in age, glabrate. Leaves oblong, runcinately lobed with round sinuses and aristate points, acute at both ends, 5–7×9–14 cm., venulose on both sides; veins about 10×2, like the midrib somewhat rosy beneath; petiole slender, tinged, 20–30 mm. long. Inflorescence and fruit?

Folia ablonga, aristato-runcinata, utrinque acuta, 5–7×9–14 cm., subtus domatiifera; petiolus gracilis, 20–30 mm. longus subrubescens.

The type is C. H. & M. T. Mueller no. 591—1933.

A moderate tree with spreading branches and deeply furrowed, dark gray or black bark. Abundant in the dense oak wood of one high slope.

Q. runcinatifolia is perhaps most closely related to *Q. Grahami* Bentham:

Leaves typically lanceolate, setaceously serrate with moderate sinuses...*Q. Grahami.*
Leaves various but with setaceous lobes and deep, rounded sinuses.
Leaves narrowly lanceolate and long attenuate, lobes entire, glabrous..*Q. cupreata.*
Leaves typically oblong or broadly lanceolate, lobes often toothed, dense tufts of axillary hairs beneath.....*Q. runcinatifolia.*

Q. runcinatifolia f. **lata** Trel. & Muell. f. nov.

A broad-leafed juvenile form comparable with those of other species of the section, the domatia-bearing leaves 4×9, 6×12, or 8×15 cm., and undulately lobed with broad shallow sinuses and shorter awns than the species.

Forma juvenilis, foliis latioribus undulato-lobatis, 4–8×9–15 cm., breviter aristatis.

The type is C. H. & M. T. Mueller no. 593—1933.

Surrounded as they are on three sides by mountainous Northern Mexico, the Chisos Mountains of Western Texas would be expected to contain numerous outposts of Mexican vegetation. There appear several novelties; their abundance is partly explained by the close proximity of the little known Sierra Madre Oriental a part of the flora of which characterizes the Chisos Mountains.

Probably this situation accounts for the origin of the two species here proposed as a new section of the genus Quercus.

Erythrobalanus—**Robustae** C. H. Muell. sect. nov.

Small or large trees with stiff branchlets from stellate hairy to glabrate; coriaceous leaves aristately toothed and from densely tomentose to variously glabrescent, relatively long petioled; fruit biennial, the cups deeply cup-shaped with glabrate blunt scales.

Ramuli rigidi ex stellato-pubescentibus glabrati; folia coriacea aristato-dentata, ex dense tomentosis varie glabrescentia; fructus biennis.

The stiff branchlets, leaves, and petioles as well as the greater pubescence and failure of the leaves to turn red in autumn distinguish the species of this section from those of the section Coccineae to which it is apparently most closely related. Autumnal coloration of leaves is a character not frequently used in the Southwest, perhaps because travel in the mountains is difficult late in the season and observations are consequently limited. The great brilliance of the foliage of *Quercus texana* var. *chisosensis* Sarg. changes entire mountain slopes from green to red. That the leaves of all the observed individuals of the section Robustae were deciduous without turning red or passed the winter in a green condition must be regarded as a character of considerable consequence. These habits were observed to be quite constant in the half dozen or more individuals of each of the two species which were examined during the autumns of two years.

Guercus robusta C. H. Muell. (Torreya **34:** 119) the type. This species was reluctantly referred to the Coccineae at the time of its description, and its relation to *Q. texana* Buckley was cited.

Quercus tardifolia C. H. Muell. sp. nov.
(Erythrobalanus—Robustae).

A small erect tree with short, stiff branches. Twigs slender (2 mm.), somewhat fluted, at first densely tomentose with fascicled hairs, glabrous or nearly so in the second year and red-brown with minute inconspicuous lenticels,

becoming finally gray with the lenticels larger but none the more conspicuous. Buds acutely fusiform, 2×3.5–4 mm., hairy at the tip, the broadly truncate scales usually split at the end, slightly hoary and often ciliate. Leaves evergreen, the new ones appearing in dense tomentum about the first of July, moderate in size (2.5–5.5×5–9 cm.), oblong-ovate to subobovate, 6 to 8-lobed by shallow or moderate sinuses, the lobes aristately tipped, entire or rarely 2-toothed, short and subright-angular like the apex, subequilaterally moderately cordate at the base, stiff coriaceous in texture, the upper surface dull blue-green, glabrate, the lower surface detachably stellate hairy; veins about 8×2, alternately passing into the teeth, hardly evident above but prominent beneath; petioles rather stiff, 1–1.5×15–20 mm., red at the base, glabrate with the leaves. Catkins? Fruit biennial; young cups very similar to the same stage on *Q. robusta*, the scales thin appressed, short-truncate, hoary or glabrate possibly indicative of the elongated narrowly rounded mature scales of *Q. robusta*.

Ramuli ex dense tomentosis glabrati; gemmae acutae 3.5–4 mm. longae, 2 mm. crassae, squamis ciliatis; folia rigida oblongo-ovata vel subobovata, 5–9 cm. longa, 2.5–5.5 cm. lata, supra ex dense stellato-tomentosis opace glabrata, subtus laxe pubescentia, lobis 6–8 plerumque integris apice aristatis; petioli rigidi 15–20 mm. longi, 1–1.5 mm. crassi; fructus biennis, cupularum juvenilium squamis tenuibus adpressis breviter truncatis.

The type was collected by the author (without number) on July 3, 1932 in the Chisos Mountains of western Texas and is deposited in the herbarium of the University of Illinois at Urbana. Co-types may be seen at the New York Botanical Garden, in the herbarium of the University of Texas at Austin, and the author's herbarium at Cuero, Texas.

The species was encountered in only a limited locality in the oak wood above "Boot Spring" at an altitude of about 7,000 feet where it grows in a small clump much after the fashion of the straight trunks and stiff, horizontal branches of young trees of *Q. marilandica* Muench. farther east. It differs from *Q. robusta* in the late appearance of its evergreen leaves, its dense tomentum, and its erect shrubby habit as opposed to the large, widespreading branches of *Q. robusta*.

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Some diatoms of Great Salt Lake

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(WITH PLATE 6 AND ONE TEXT-FIGURE)

This study of the diatom flora of Great Salt Lake was made in connection with the investigations of Dr. A. J. Eardley, of the University of Michigan, on the geological conditions of Great Salt Lake. This lake, which is 4200 feet above sea level, is located in the northwestern part of Utah. Three fresh water rivers, the Jordan, the Weber, and the Bear rivers empty into it. The water, however, has a salt concentration approximately six times that of the sea. This concentration, due largely to the fact that the lake has no outlet, is so high that very few organisms can live in it.

A large body of fresh water, known as Lake Bonneville, occupied the bed of Great Salt Lake in Quaternary times. Its surface was more than a thousand feet above the present level of Great Salt Lake, and it covered a much larger area which was approximately equal to that of Lake Michigan. Due to evaporation and the closing of its drainage system, Lake Bonneville became more and more salt. Its salt concentration was for a long but indefinite period near that of the sea.

It was believed that the presence of diatoms in the various deposits might tell something of the past history of the lake. By means of a Musselman Peat Sampler, diatoms were taken from several depths. Surface samples were also collected.

The diatoms were cleaned by the acid method. Sometimes it was necessary to use soap solution in order to separate them from the clay. They were mounted in hyrax. A description of the samples taken and the various species found in each is given below. The symbols used for the various localities are those which Eardley employed in his paper. An appended map (after Eardley) shows the location of the stations from which various samples were taken.

Sample A. Blue-gray mud, under oolites. Collected at Rozell Point which is located on the northeastern shore of the lake.

Cyclotella striata (Kütz.) Grun.	Brackish water (marine, Boyer)
Cymbella cymbiformis (Kütz.) Breb.	Fresh water
Denticula elegans Kütz.	Fresh water
Diploneis oculata (Breb.) Cl.	Fresh water
Diploneis ? (a form intermediate between D. puella and D. elliptica)	
Epithemia intermedia Frische (acc. Pascher)	Fresh water
Epithemia zebra? (Ehr.) Kütz.	Fresh and brackish water
Fragilaria mutabilis (W. Sm.) Grun.	Fresh water
Melosira distans (Ehr.) Kütz.	Fresh water
Melosira granulata (Ehr.) Ralfs	Fresh water

Navicula bacillum Ehr.	Fresh water
Navicula bacillum v. lepida (Greg.) Cl.	Fresh water
Navicula cincta (Ehr.) Kütz. acc. V.H.	Fresh and brackish water
Navicula cryptocephala Kütz.	Fresh water, rarely brackish
Navicula peregrina (Ehr.) Kütz.	Brackish water
Navicula rhynchocephala v. amphiceros (Kütz.) Cl.	Fresh and brackish water
Nitzschia amphibia Grun.	Fresh water
Nitzschia apiculata (Greg.) Grun.	Euryhaline
Nitzschia epithemoides Grun.	Brackish water
Nitzschia subtilis v. paleacea Grun.	Fresh and brackish water
Pinnularia borealis Ehr.	Fresh water
Scoliopleura peisonis Grun.	Brackish water
Surirella striatula Turpin	Euryhaline
Synedra ulna (Nitzsch.) Ehr.	Fresh water

Opephora—? This is an interesting form of which I found only a few specimens. Due to the shape and type of striae, I have placed it in this genus. Valve linear, clavate; length 31 microns, breadth 6–7 microns. Striae 8 in 10 microns. Plate 1, figs. 1, 2, 3.

There are many whole specimens as well as fragments of diatoms in this sample. The species characteristic of fresh to brackish water are most abundant as to numbers of individuals. There are, however, fresh water species represented. Also, there are forms which live in relatively high salt concentrations and are usually found in brackish to marine conditions.

These results support the geological findings that extensive swamps existed in this region in the very recent geologic past. These swamps, no doubt, had water of varying salt concentrations.

Sample Aa. Light gray mud, somewhat coarse, taken under fourteen feet of water, from the surface mud. Collected one mile east of Carrington Island, which is located in the southwest part of the lake. No diatoms.

Sample B. Blue-gray mud from Rozell Point, which is on the northeast shore of the the lake, taken under two feet of water and twenty feet below surface muds by means of a Musselman peat sampler.

Denticula tenuis Kütz.	Fresh water
Diploneis elliptica (Kütz.) Cl.	Fresh water (also brackish-Boyer)
Epithemia argus v. alpestris (W. Sm.) Grun.	Euryhaline
Fragilaria brevistriata Grun.	Fresh water
Fragilaria mutabilis (W. Sm.) Grun.	Fresh water
Melosira granulata (Ehr.) Ralfs	Fresh water
Navicula cincta (Ehr.) Kütz. acc. V.H.	Fresh and brackish water
Navicula radiosa v. tenella (Breb.) V.H.	Fresh water
Nitzschia hungarica Grun.	Brackish water (also fresh-Boyer)
Pinnularia Brebissoni (Kütz) Cl.	Fresh water
Surirella striatula Turpin	Euryhaline
Surirella angusta Kütz	Fresh water
Synedra affinis v. acuminata Grun.	Fresh water
Synedra affinis v. lancettula Grun.	Fresh water

Many fragments of *Pinnularia* spp. and *Cymbella* spp. were found. The genera *Fragilaria* and *Denticula* were dominant. These findings indicate

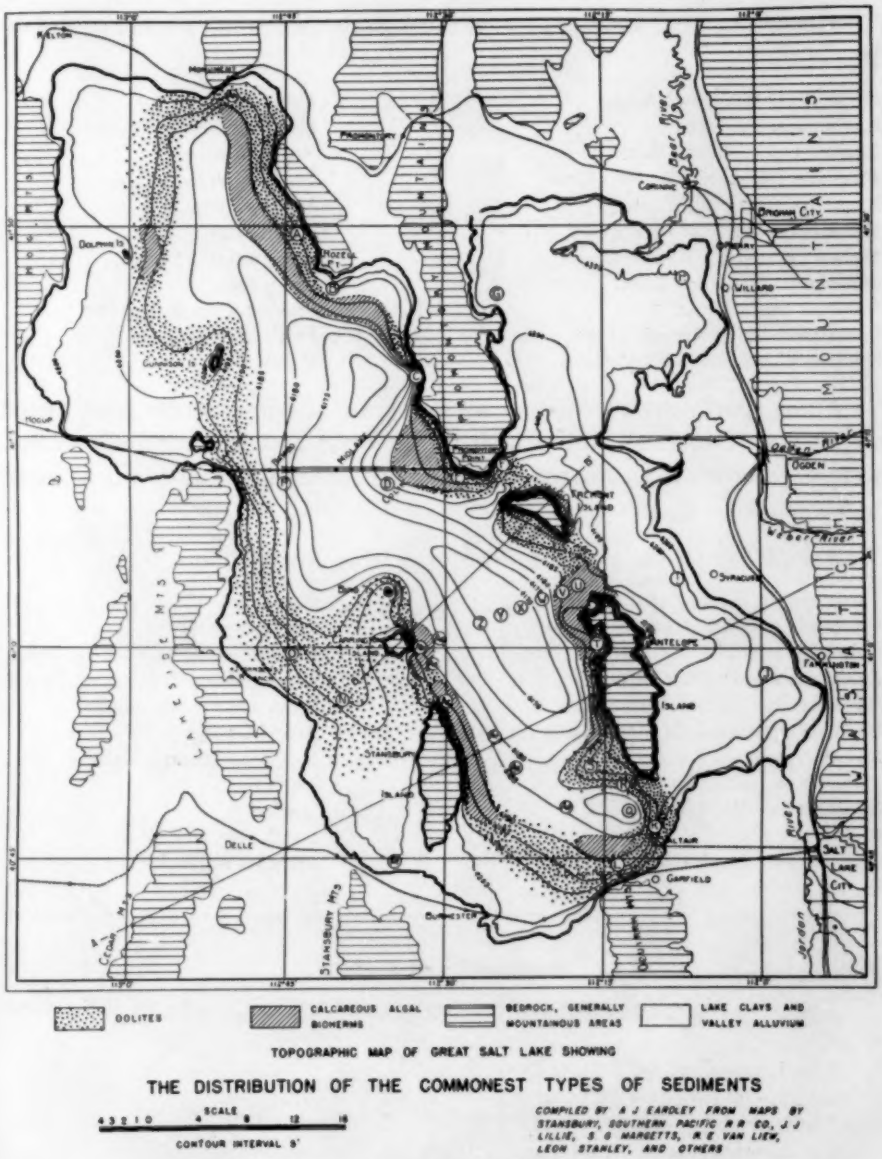

OOLITES
CALCAREOUS ALGAL BIOHERMS
BEDROCK, GENERALLY MOUNTAINOUS AREAS
LAKE CLAYS AND VALLEY ALLUVIUM
TOPOGRAPHIC MAP OF GREAT SALT LAKE SHOWING
THE DISTRIBUTION OF THE COMMONEST TYPES OF SEDIMENTS
SCALE
CONTOUR INTERVAL 5'
COMPILED BY A J EARDLEY FROM MAPS BY STANSBURY, SOUTHERN PACIFIC R R CO., J J LILLIE, S G MARGETTS, M E VAN LIEW, LEON STANLEY, AND OTHERS

Fig. 1. Showing where the samples were obtained.

that the water at this depth was for the most part fresh. However, two euryhaline forms and three fresh to brackish water form were found. This might indicate a brackish tendency. According to the rate of deposit of

sediment in the lake, as determined by Eardley, these samples were about ten thousand years old.

Sample B_2. Fine, blue-gray mud taken from around oil seep craterlet at Rozell Point.

Cyclotella comta (Ehr.) Kütz.	Fresh water
Epithemia sorex Kütz.	Fresh and brackish water
Eunotia gracilis (Ehr.) Rabh.	Fresh water
Fragilaria Harrisonii (W. Sm.) Grun.	Fresh water
Fragilaria mutabilis (W. Sm.) Grun.	Fresh water
Melosira distans (Ehr.) Kütz.	Fresh water
Melosira granulata (Ehr.) Ralfs	Fresh water
Melosira italica (Ehr.) Kütz.	Fresh water
Navicula cincta ? Ehr.	Fresh and brackish water
Pinnularia viridis (Nitzsch.) Ehr.	Fresh water
Stephanodiscus astrea (Ehr.) Grun.	Euryhaline

Many specimens were found. Most of these species indicate fresh water conditions. Two fresh to brackish water forms and one euryhaline form were encountered. Evidently the mud was forced up from a much lower level.

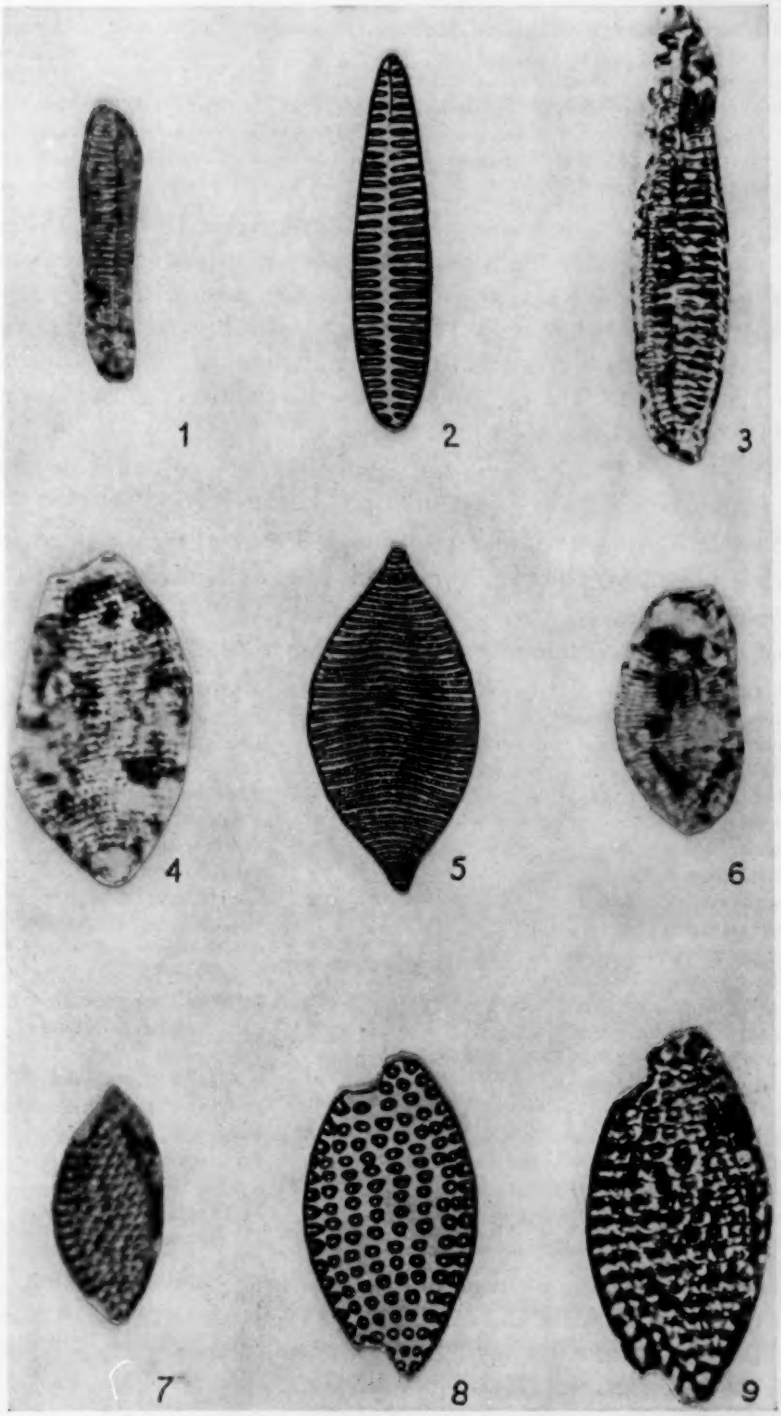
Sample B_3. Green-gray craterlet mud from Rozell Point.

Cocconeis placentula Ehr.	Euryhaline
Epithemia musculus Kütz.	Brackish water
Epithemia musculus v. constricta (Bréb.) V.H.	Brackish water (Marine-De-Toni)
Epithemia zebra ? (Ehr.) Kütz.	Fresh and brackish water
Navicula cincta (Ehr.) Kütz. acc. V.H.	Fresh and brackish water
Navicula cryptocephala v. pumilla (Grun.) Cl.	Brackish water
Navicula pygmaea Kütz.	Fresh and brackish water
Nitzschia amphibia Grun.	Fresh water
Nitzschia socialis ? Greg.	Marine
Rhopalodia gibberula (Ehr.) O. Müll.	Euryhaline
Scolioplcura peisonis Grun.	Brackish water

Explanation of Plate 6

The photomicrographs and drawings are often of different specimens of the same species.

Fig. 1. Opephora—? (×1000).
Fig. 2. Opephora—? (×1630).
Fig. 3. Opephora—? (×1600).
Fig. 4. Nitzschia sp.? (×1600).
Fig. 5. Nitzschia sp.? (×1550).
Fig. 6. Nitzschia sp.? (×1000).
Fig. 7. Nitzschia—? (×1000).
Fig. 8. Nitzschia—? (×1600).
Fig. 9. Nitzschia—? (×1600).



PATRICK: DIATOMS OF GREAT SALT LAKE

Nitzschia punctata ? (W. Sm.) Grun. The specimens which I found are closely allied to, if not the species *Nitzschia puncata* (W. Sm.) Grun. The main difference is in the number of striae. They are more numerous, averaging about 17 in 10 microns. Plate 6, figs. 4, 5, 6.

Nitzschia—? This is nearest to *Nitzschia granulata* Grun. However the double row of puncta in the keel are not evident. The valve is convex, elliptical with more or less acute ends. Length about 30 microns. Breadth is 15 microns. Striae are composed of large puncta, about six striae in 10 microns. Plate 6, figs. 7, 8, 9.

In this sample were many specimens of *Nitzschia*. However, the markings on the valves of many had been obliterated. Many specimens of *Epithemia musculus* Kütz., *Navicula cincta* Ehr., and *Scoliopleura peisonis* Grun. were found, which indicate more or less brackish water. As the water at this point is now very salt, it is evident that the mud was forced up from a lower depth. There is geologic evidence that fresh to brackish water swamps existed at this point in the past.

Sample D. Slightly coarse tan mud collected one half mile west of Colin in ten feet of water. No diatoms.

Sample F. Blue-gray and tan mud collected at Promontory Point, which is a southern point of Promontory Range. No diatoms.

Sample G. Tan clay, somewhat dried, no water cover at present, collected midway, east side of Promontory Range.

Amphora proteus Greg.	More or less euryhaline
Caloneis amphisbaena (Bory) Cl.	Fresh and brackish water
Cocconeis scutellum? Ehr.	Brackish and marine water
Cyclotella operculata Kütz.	Fresh water (brackish-De-Toni)
Cymbella aspera (Ehr.) Cl.	Fresh water
Denticula elegans Kütz.	Fresh water
Denticula thermalis Kütz.	Warm water
Epithemia sorex Kütz.	Fresh and brackish water
Epithemia sorex v. gracilis Hust.	Euryhaline
Epithemia turgida (Ehr.) Kütz.	Fresh and brackish water
Epithemia zebra v. saxonica (Kütz.) Grun.	Fresh water
Fragilaria mutabilis (W. Sm.) Grun.	Fresh water
Hantzschia amphioxys (Ehr.) Grun.	Fresh and brackish water
Navicula cincta Ehr.	Fresh and brackish water
Navicula radiosa v. tenella (Breb.) V.H.	Fresh water
Navicula viridula v. avenacea (Breb.) Grun.	Fresh and brackish water
Nitzschia hungarica Grun.	Fresh and brackish water
Nitzschia parvula W. Sm. acc. Schönfeldt	Fresh and brackish water
Pinnularia Brebissoni (Kütz.) Cl.	Fresh water
Pinnularia viridis (Nitzsch.) Ehr.	Fresh water
Rhopalodia gibba (Ehr.) Müll.	Fresh and brackish water
Surirella striatula Turpin	Euryhaline

There is a mixture of fresh and brackish water forms. This mud has been the bed of some of the springs along the mountain base. There are numerous fresh water springs here, some of which are slightly sulphurous, while others are saline.

Sample H. Blue-gray and tan mud taken from fresh water canal, northeastern part of lake. Collected west of Perry, near the dike to Bird Refuge.

Amphora ovalis (Bréb.) Kütz.	Fresh water
Anomoeoneis polygramma (Ehr.) Cl.	Brackish water
Anomoeoneis sculpta (Ehr.) Cl.	Fresh and brackish water
Anomoeoneis sphaerophora (Kütz.) Pfitz.	Fresh and brackish water
Caloneis formosa (Greg.) Cl.	Brackish and marine water
Cymbella cistula (Hemphr.) Grun.	Fresh water
Diploneis oculata (Breb.) Cl.	Fresh water
Diploneis ovalis (Hilse) Cl.	Fresh and brackish water
Epithemia turgida v. granulata (Ehr.) Grun.	Fresh and brackish water
Epithemia zebra (Ehr.) Kütz.	Fresh and brackish water
Gomphonema longiceps v. subclavata Grun.	Fresh water
Mastogloia Dansei Thw.	Brackish or almost fresh water
Navicula cincta (Ehr.) Kütz. acc. V.H.	Fresh and brackish water
Navicula cryptocephala v. pumila (Grun.) Cl.	Brackish water
Navicula oblonga Kütz.	Fresh or slightly brackish water
Navicula peregrina (Ehr.) Kütz.	Brackish water (salt water-Hustedt)
Navicula pupula Kütz.	Fresh water
Navicula salinarum Grun.	Euryhaline
Nitzschia apiculata (Greg.) Grun.	Euryhaline
Nitzschia punctata (W. Sm.) Grun.	Euryhaline
Nitzschia punctata v. elongata ? Grun.	Probably euryhaline.
Nitzschia sigmoidea ? (Nitzsch.) W. Sm.	Fresh water
Pinnularia viridis (Nitzsch.) Ehr.	Fresh water
Pleurosigma delicatulum W. Sm.	Brackish and occasionally fresh,—De-Toni reports it from a marine locality
Rhopalodia gibba (Ehr.) Müll.	Fresh and brackish water
Scoliopleura peisonis Grun.	Brackish water
Surirella ovata Kütz.	Fresh water
Surirella ovata v. utahensis Grun.	Fresh and brackish water
Surirella striatula Turpin	Euryhaline
Synedra acus Kütz.	Fresh and brackish water

In this list we have a mixture of truly fresh water forms along with with fresh to brackish water species. Geological evidence points to the fact that this sample for the most part was laid down under brackish water conditions when the lake was at a much higher level. To the surface has been added the shells of fresh water diatoms now living in the fresh water canal. This, then, accounts for the curious mixture.

Sample I. Gray mud, no water cover, near eastern line of lake. Collected three miles west of Syracuse. The lake has recently withdrawn. No diatoms.

Sample J. Gray mud, somewhat dried, near the southeastern line of the lake. No water cover at present. Collected at Farmington about one foot below surface of mud. No diatoms.

Sample K. Blue-gray mud under oolites from southern part of lake. Collected at Salt Air. No diatoms.

Sample M. Tan mud from southwestern part of lake. Collected on lake bottom now dry, between Stanbury Island and the railroad track to southeast. No diatoms.

Sample O. Tan-gray mud, somewhat dried, no water cover at present from western side of lake. Taken eight inches below the surface at a point east of Johnson's Ranch and two miles inland from the present water line.

Caloneis silicula v. minuta (Grun.) Cl.	Fresh water
Cyclotella Meneghiana Kütz.	Fresh water
Cymbella cistula (Hemphr.) Grun.	Fresh water
Epithemia argus (Ehr.) Kütz.	Euryhaline
Epithemia argus v. alpestris (W. Sm.) Grun.	Euryhaline
Epithemia zebra (Ehr.) Kütz.	Fresh and brackish water
Fragilaria mutabilis (W. Sm.) Grun.	Fresh water
Hantzschia elongata ? (Hantzsch.) Grun.	Fresh water
Melosira arenaria Moore	Fresh water
Melosira crenulata (Ehr.) Kütz.	Fresh water
Navicula gracilis Ehr.	Fresh water
Pinnularia Brebissoni (Kütz.) Cl.	Fresh water
Surirella striatula Turpin	Euryhaline

There are many fragments as well as whole specimens in this sample. The predominant species are fresh water forms, although one fresh to brackish and several euryhaline species are found. This sample is hard to explain from the apparent geological history of the lake. The most probable explanation is that a thousand years ago there may have been numerous fresh water springs in this region, such as exist to-day on the east shore of Antelope Island, which run out on the lake bottom. Thus the existence of these fresh water forms may be explained.

Sample Q. Slightly coarse, tan-gray mud from the southern part of the lake. Collected four miles northwest of Salt Air in twenty feet of water. Only a very few broken fragments of diatoms were found. They were not large enough to identify as to species. These fragments were probably brought in by extraneous forces.

Sample T. Two samples were taken in White Rock Bay on the west side of Antelope Island, in the southeastern part of the lake. The samples were taken from the surface muds as well as three feet below the surface. No diatoms were found. The sediment is believed to have been deposited faster here than in other parts of the lake.

Sample Y. This sample was taken in the middle of the lake, southern part, one mile east of sample Z. No diatom flora was evident. A few frag-

ments of specimens belonging to the genera *Fragilaria*, *Melosira*, *Pinnularia*, and *Synedra* were found. They were so fragmentary that it is evident that they were brought in by extraneous forces.

Sample Z. Tan-gray mud was taken in the middle of the lake under twenty-five feet of water. It was taken east of Carrington Island. No diatom flora was evident. As in sample Y a few fragments were found which were evidently brought in by extraneous forces. Samples Y and Z were taken from the deepest part of the lake.

The results of these studies seem to indicate several interesting facts. The deepest samples taken, which were those by means of the peat borer, support the theory that a fresh water lake formerly occupied the region where Great Salt Lake now is. Ehrenberg (1870), and others noted the presence of fresh water deposits in Great Salt Lake. Eardley[1] states that the rate at which sediment is deposited is about six feet in ten thousand years. This rate varies in different parts of the lake.

The craterlet mud taken from the Rozell Point region is evidently clay which has been brought up from lower depths in the building of craterlets. The finding of these fresh and brackish water diatoms supports the geological theory of Eardley that swamps existed here in Pleistocene or early Post-pleistocene times.

Lake Bonneville, which was the fresh water lake that formerly occupied this region, gradually became more and more salt due to the lack of drainage and to evaporation. Therefore at one time it must have had much the same salt concentration as the sea, and this condition probably existed for a long but indefinite period. Moore (1899) has shown that the chemical composition of the water of Great Salt Lake is similar to that of the sea. Marine diatoms have been found to flourish in properly diluted water from the Great Salt Lake. In view of these facts it is interesting to note that truly marine forms seem never to have established themselves in the lake. Ehrenberg (1870) speaks of the rarity of marine forms. Of the few marine forms which he describes from this lake, that I have been able to trace, all, except *Coscinodiscus radiatus* Ehr., have since been found to be also brackish water forms. My studies also point to the fact that a marine diatom flora was never established in the lake.

No diatom flora is found living in the lake proper to-day. Daniels (1917) reports two diatoms from the denser waters of the lake. He states that they flourished when the concentration was reduced. He did not identify them as to species, and only approximately as to genera. My examination of the above mentioned surface muds, as well as of samples of living

[1] Eardley, A. J. Unpublished observations.

algae, which were taken from the lake proper, showed no evidence of a diatom flora. Living forms reported from this lake have been found, no doubt, in the surrounding brackish marshes and river deltas which have a much lower salt concentration.

The absence of living diatoms in the lake proper is to be expected in view of the fact that so few organisms can withstand the high salt concentration which exists in the present lake.

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INDEX TO AMERICAN BOTANICAL LITERATURE
1931–1935

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